SOCIAL ORGANISATION, ECOLOGY AND CONSERVATION OF *LORIS TARDIGRADUS TARDIGRADUS* (LORISIFORMES; PRIMATES)

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This thesis is dedicated to my husband, Adin S. Beresford, without whom this thesis would not have been completed.

This dissertation is the result of my own work, and includes nothing, which is the outcome of work done in collaboration. This dissertation does not exceed the word limit of 100,000 words.

ABSTRACT

Loris tardigradus tardigradus, the red slender loris, is a small nocturnal primate inhabiting the rainforests of Sri Lanka. This study provides new information on the natural history, social organisation and ecology of this endangered strepsirrhine, from which conservation action plans are derived. The study was conducted in Masmullakele, a 290ha forest reserve. Vegetation, diurnal and nocturnal surveys were conducted between October 2004 to August 2005 and the radio-tracking study from August 2005 to July 2006. Seventeen lorises were radio-tracked for 339 nights, and observed for 579hrs. Average home range size was 3.2ha $\pm$ 1.7, and core area size 2.2ha $\pm$ 1.1 with no significant inter- or intra-sexual differences. Overlap was significantly higher inter-sexually than intra-sexually. Lorises formed spatial pairs with coinciding home ranges and little overlap with neighbouring animals and had high indices of territoriality. Lorises were social 21.4% of the time, with neutral interactions being the most frequent, and direct negative interactions the least. 'Paired' lorises had a significantly higher degree of cohesiveness and sociality than unpaired lorises. Lorises did not use anthropogenically disturbed habitats and preferred interior forest, although they used patch perimeter habitat (forest edge microhabitat) significantly more than was available. Temperature had a significant positive effect on activity, whilst a significant negative correlation was found between rainfall and home range size. There was indication that lorises may have had two breeding seasons in that year based on time of oestrous and births, and changes in ranging patterns. Lorises have a complex social organisation. The spatial system is unimale-unifemale, and the social system, gregarious or dispersed depending on degree of spatial overlap. The mating system does not appear to be monogamous. Possible mating systems are: 1) serial monogamy; 2) long-term pair-bond with the occurrence of EPCs; 3) formation of social and spatial pair but with a polygynous mating system. Conservation actions proposed are to: increase baseline data on *L. t. tardigradus* across the Wet Zone, continue this study's research objectives, conduct process-based models, decrease fragmentation within small forests and create a network of protected forests.

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LIST OF ACRONYMS AND ABBREVIATIONS (in alphabetical order)

A	Adult
C	Circumference of home range
CBH	Circumference at Breast Height
CI	Cole's Index of association
D	Index of Defendability
d	mean nightly path length
DBH	Diameter at Breast Height
EPC	Extra Pair Copulation
h	Smoothing factor
IID	Inter-Individual Distance
IVI	Importance Value Index
KDE	Kernel Density Estimators
KW	Kruskal-Wallis test
LSCV	Least Squares Cross Validation
M	Fraction Monitoring Index
MCP	Minimum Convex Polygon
MPFR	Masmullah Proposed Forest Reserve
MWU	Mann-Whitney U test
N	Individual's needs
NII	Night Illumination Index
NL	No Loris area
NST	North-South Trail
PVA	Population Viability Analysis
R	Amount of available resources
RTI	Range Traversing Index
SA	Subadult
SP	Stream Path
SS(1,2,3)	Study Site area (1,2,3)
TTI	Time to Independence
VP(1,2,3)	Village Path (1,2,3)

CHAPTER 1 GENERAL INTRODUCTION

1.1. INTRODUCTION

The dwindling lowland rainforests of Southern Sri Lanka hide a little-known primate, the red slender loris (*Loris tardigradus tardigradus*), that has been classified as Endangered C2a(i) by the IUCN (2008) with around 1500 animals left across 3000 hectares of highly fragmented forest in the Wet Zone (Mill, 1995; Myers *et al.*, 2000). One of the first steps towards preventing extinction of a species is to gather baseline information on population dynamics, and their social and behavioural ecology, so that appropriate conservation measures may be taken based on a better understanding of the species biology and behaviour. Although short-term surveys have been conducted to assess the distribution and habitat needs of *L. t. tardigradus* (Nekaris and Jayewardene, 2003, 2004; Nekaris *et al.*, 2005) relatively little is known on its behavioural ecology and social organisation.

Thus, I set out to conduct the first long-term radio-tracking study of *L. t. tardigradus*, between October 2004 and August 2006, in a proposed forest reserve known locally as Masmullakele, and from here on, referred to as MPFR (Masmullah Proposed Forest Reserve). The broad aims of this study were:

1) To describe the slender loris population of MPFR, including density, sex ratio and number of mature and immature individuals, and describe MPFR, its floristic composition and abundance estimates of other mammal species.

2) To investigate the social organisation of *L. t. tardigradus* using quantitative data on spatial and social patterns.

3) To evaluate the degree of behavioural and ecological plasticity exhibited by *L. t.*

tardigradus based on observed patterns of habitat and microhabitat use and responses to abiotic factors.

4) To propose conservation goals for *L. t. tardigradus* and avenues for future research based on the findings from the first three aims of this study.

In this introduction I present background information on Sri Lanka and on the taxonomy, distribution and conservation status of slender lorises, from here on referred to as lorises. I also briefly document what is currently known of the behaviour and ecology of lorises, both in the wild and in captivity and finish off by describing in more detail the structure of the thesis.

1.2. SRI LANKA: AN OVERVIEW

The island nation of Sri Lanka covers 65610 km² and is separated from India's south-eastern tip by the 60 kilometre Palk Strait and Gulf of Mannar. It is inhabited by approximately 18.5 million people (FRA, 2001) and despite being one of the smallest countries in Asia, arguably harbours greater biological diversity per unit area than any other Asian country (Braatz, 1992). Much of this diversity is endemic and presumably a reflection of the island's separation from the Indian subcontinent since the late Mesozoic (Pabla and Mathur, 1999). Despite its geographical proximity to India, Sri Lanka supports a surprising level of endemism (Table 1.1).

Table 1.1 Percentage endemism in Sri Lanka

	Flowering plants	Reptiles	Amphibians	FW fish	Birds	Mammals
Endemic species (%)	28 [1]	52 [1 2]	64 [1 2]	41 [1 2]	10 [1 3]	15 [1]

[1] IUCN, Sri Lanka (2000), in: Sri Lanka: State of the Environment Report (2001), [2] Senanayake *et al.* (1977); [3] Crusz (1986), Gunatilleke and Gunatilleke (1983)

Forests are the predominant vegetation in Sri Lanka, varying from ever-wet lowland and montane rainforests to dry evergreen and thorn forests, interspersed by a complex network of wetlands, freshwater, coastal and marine ecosystems (FRA, 2001). In 1956 natural forests covered nearly 44% of Sri Lanka's land area (Soussan and O'Keefe, 1985). Remote sensing information shows that by 1983 natural closed-canopy forest covered just 18.5% of the island's area (Green and Gunawardene, 1997; Ratnayake *et al.*, unpublished). Most of the remaining forest is in the Dry Zone and only 3% remains in the Wet Zone. In addition, the presence of illegal paddy fields and progressive encroachment of agricultural land, have fragmented and isolated the remaining forest patches, thus resulting in Sri Lanka's total forest cover consisting in few tracts of forest larger than 10000 hectares (IUCN/FAO, 1997). Major causes of deforestation and forest degradation are fuel-wood gathering, permanent agriculture, shifting cultivation, tree plantations, fire, and mining for gem stones, urbanisation and timber felling (Myers *et al.*, 2000; Wickramasinghe *et al.*, 1996; Maheswaran and Gunatilleke, 1988; Hewawasam *et al.*, 2003; Bogahawatte, 2003)

The Wet Zone of Sri Lanka covers approximately a quarter of the country and is characterised by lowland rainforest, extending up to 1000 metres, and sub-montane and montane rainforest, occurring above 1000 metres. As well as holding the highest level of biodiversity and endemism in Sri Lanka (Gunatilleke and Gunatilleke, 1983),

the Wet Zone also is the region of highest human population density, holding nearly 60% of the country's 18.5 million inhabitants (FRA, 2001). The Intermediate Zone is characterised by moist semi evergreen forests, separating the Wet Zone from the Dry Zone. This transition belt shows its own characteristic species as well as some common to the adjacent zones (FRA, 2001).

1.3. THE STUDY SPECIES: AN OVERVIEW

1.3.1. Taxonomy

Slender lorises have been classified both as Prosimii and Strepsirrhini. In this thesis, the term strepsirrhine will be used to describe primates traditionally belonging to the Prosimii who share symplesiomorphies and morpho-anatomical synapomorphies (Fleagle, 1999). Following this classification, the Tarsiiformes are grouped with the suborder Haplorhini, and the Lemuriformes, Lorisiformes and Chiromyiformes with the suborder Strepsirrhini (Goodman *et al.*, 1998; Schmitz *et al.*, 2001, Poux and Douzery, 2004). For the purpose of the thesis however, whenever tarsiers are to be 'grouped' with strepsirrhines, the term prosimian will be used.

The lorises are part of the family Lorisidae, which includes also the African Galaginae and Perodicticinae (Grubb *et al.*, 2003; Nekaris and Bearder, 2007). The galagines can be found throughout most of Africa, south of the Sahara and accordingly, occupy a wide range of habitats. Currently, twenty-four species are recognised (Grubb *et al.*, 2003; Isaac *et al.*, 2004; Perkin, 2001b; Perkin *et al.*, 2002; Perkin, 2007), a number that has drastically increased from the original taxonomic classification in 1979 of six species (Petter and Petter-Rousseaux, 1979). The perodicticines include two morphotypes, the gracile form commonly referred to as angwantibo, which currently

comprises two species and the robust form commonly referred to as the potto, which is currently thought to comprise three species and five subspecies (Pimley, 2002; Roos *et al.*, 2004; Kingdon, 1997). The pottos and angwantibos are found in a variety of habitats, from primary forest through swamp, lowland and mid-altitude montane forests to riverine and semi-moist deciduous forests.

In Asia, the lorisines also include a robust form, the slow loris (*Nycticebus* spp.) and a gracile form, the slender loris (*Loris* spp.) (Hill, 1953). Based on genetic, morphological and behavioural data, the slow loris is currently thought to comprise five species (Groves and Maryanto, 2008; Roos *et al.*, 2004; Nekaris and Jaffe, 2005), which have been independently assessed in the IUCN Red List (Nekaris and Nijman, 2007).

Hill (1933, 1953) recognised six subspecies of slender lorises based on pelage colour and other morphological variations, whilst the more recent taxonomic classification by Groves (2001), based on morphometric differences, results in two distinct species, *Loris tardigradus,* commonly referred to as the red slender loris and *Loris lydekkerianus* known as the grey slender loris (Groves, 2001). The red slender loris comprises two subspecies, *Loris tardigradus tardigradus* and *Loris tardigradus nycticeboides.* The former is morphologically distinct from other subspecies in being the smallest form, having a long jaw and relatively broad bicanine and bizygomatic width (Groves, 2001) and also having relatively rapid locomotion in comparison to other slender loris forms (Nekaris and Stevens, 2005). The taxonomic status of *L. t. nycticeboides* remains unclear due to the fact that only four museum specimens exists and no living specimens have been caught and measured. Based on the skull measurements alone though, it is recognised as the most distinct of all and may be a separate species (Groves, 1998).

1.3.2. Distribution and Conservation Status

The red slender loris is restricted to the south-western and montane regions of Sri Lanka (*L. t. tardigradus* and *L. t. nycticeboides* respectively), whereas the grey slender loris can be found in the northern and central parts of Sri Lanka (*Loris lydekkerianus nordicus* and *Loris lydekkerianus grandis*) (Hill, 1933; Phillips, 1935; Petter and Hladik, 1970; Jenkins, 1987; Nekaris, 2003b; Brandon-Jones *et al.*, 2004; Nekaris and Jayewardene, 2004) and in South-East India (*Loris lydekkerianus malabaricus* in the south-western parts of India and *Loris lydekkerianus lydekkerianus* in the South-East parts of India) (Kar Gupta, 1995; Singh *et al.*, 1999; 2000; Lakshmi and Mohan, 2002; Brandon-Jones *et al.*, 2004; Kumara *et al.*, 2004) (Figure 1.1). The Indian forms are currently listed as Near Threatened , whilst three of Sri Lanka's slender lorises are rated as Endangered (A2cd + 4cd) based on habitat loss alone (Hilton-Taylor, 2002). The montane slender loris, *L. t. nycticeboides*, is restricted to the fragile and endangered cloud forest of Sri Lanka's Horton Plains and has been listed by the IUCN as one of the top 25 most endangered primates in the world (Hilton-Taylor, 2002; Nekaris and Perera, 2007). Over the past decades very few sightings had been recorded, let alone published, but in 2002, two sightings of *L. t. nycticeboides* confirmed its presence at the Horton Plains National Park (HPNP) (Nekaris, 2003b) and a more recent study conducted by a team of Sri Lankan researchers has yielded equally few sightings despite intensive surveys conducted over a period of one year, and population density was estimated at 0.02 per square kilometre (Gamage, pers.comm.).

Figure 1.1. General distribution of *Loris* in Sri Lanka based on the distribution map created by Schulze and Meier, 1995, and data from Bernede and Gamage (2006). Areas between *Loris tardigradus tardigradus* and *Loris lydekkerianus grandis* may have either both species, or an intermediate form.

1.3.3. Ecology and Habitat Use

Within Sri Lanka, the slender loris inhabits environments ranging from montane cloud forests, to thorny scrub forest, whilst *L. t. tardigradus* is limited to the diminishing rainforests of South-western Sri Lanka. Most of what is known of this species relates to habitat use and, according to Nekaris and Jayewardene (2003), this species tends to avoid human settlements such as home gardens and agricultural land, thus preferring the forest interior. The grey slender loris, *L. lydekkerianus*, on the other hand tends to occur with a higher relative abundance in plantations, cultivated areas and villages (*L. l. lydekkerianus*: Singh *et al.*, 1999), prefers disturbed habitats such as cardamon plantations and scrub forests (*L. l. malabaricus:* Kar Gupta, 2007), and is often seen using village gardens, road edge and plantations (*L. l. nordicus*: Nekaris and Jayewardene, 2003).

Even fewer studies report data on the behaviour of slender lorises. Nevertheless, several studies have looked at activity budgets of *L. lydekkerianus* in captivity (Subramoniam, 1957; Johnson, 1984; Goonan, 1993; Schulze and Meier, 1995; Bernede, 2002) and in the wild (Nekaris, 2000; Radakrishna, 2001). A study on captive *L. l. malabaricus* reported the latter to be active in the day (Subramoniam, 1957), whilst a long-term field study on free ranging *L. l. lydekkerianus* also noted diurnal activities, which occurred at the sleeping site when disturbed (Bearder *et al.*,. 2002). However, generally, the slender loris is considered completely nocturnal and no reports of diurnal activities, as seen in cathemeral primates, have been reported. Nothing is currently known of the way in which *L. t. tardigradus* allocates time to different activities, the factors that may influence its activity budget, or whether activity profiles vary in relation to sex or age. Such information is vital in evaluating

the range requirements and potential degree of behavioural plasticity exhibited by this species.

1.3.4. Social Organisation

Social organisation can be described as comprising three components: the spacing system, represented by the spatial and temporal distribution of individuals, the social system, described by the behaviour and relationships between individuals within a group, and finally, the mating system, defined by the reproductive interactions between individuals (Sterling, 1993). The latter is possibly the most difficult component to study without the use of genetic analyses, whilst the investigation of the spacing system has been greatly facilitated by the advancements of radio-tracking technology (Sterling and Radespiel, 2000). Thus, ranging patterns exhibited within a population have often been used as a way to elucidate the characteristics of a species' social organisation (Sterling and Radespiel, 2000; Bearder and Martin, 1980; Bearder, 1987; Harcourt and Nash, 1986).

One of the earlier reviews of diversity in social organisation amongst prosimians as revealed by the use of radio-telemetry, was that of Bearder (1987), who described five different types of social systems (social organisation) based on work conducted on lorisids (based on his own work and that of Charles-Dominique, 1977), tarsiers (based on the studies by Niemitz, 1984) and other nocturnal primates (based on studies of lemurs by Martin, 1972; Charles-Dominique, 1978; and owl monkeys (*Aotus*) by Wright, 1978). These types were classified using the level of inter- and intra-sexual territorial overlap and sleeping associations between members of a population.

Mueller and Thalmann (2000) further classified social organisation by separately defining spatial systems, and social systems. Thus, they describe four basic patterns of spatial systems based on the pattern of overlap between individuals' home ranges (the general concept of 'home range' is based on the definition by Burt (1943:351) "that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range". Thus, home ranges could follow one of four different patterns of overlap:

1. The home ranges of a male and a female coincide.
2. The home range of a male overlaps that of several females and vice versa.
3. The home range of a male overlaps those of several females exclusively.
4. The home range of a female overlaps that of several males.

They describe prosimians as forming one of three social grouping patterns. These are:

1. Cohesive (or gregarious) groups: this refers to groups of animals that maintain a tight social network and where movements are coordinated between individuals (two or more). For example, in the woolly lemur (*Avahi* spp.) adult pairs forage and sleep together and coordinate their movements (Harcourt, 1991) and spectral tarsiers (*Tarsius spectrum*) are gregarious throughout the night and form sleeping groups (Gursky, 2000, 2002).
2. Dispersed groups that form 'social networks' include animals that forage mainly alone but interact with other conspecifics and form sleeping groups. For example, in the fork-marked lemur (*Phaner furcifer*) pairs form permanent sleeping groups but do not forage together, and despite having frequent

interactions, show a low degree of cohesiveness (Schulke and Kappeler, 2003).

3. Solitary animals that have no interactions with other individuals, other than during the breeding season. A primate known with this type of grouping is the aye-aye (*Daubentonia madagascarensis*) in which adults sleep and forage solitarily and only come together during the mating season (Sterling and Richard, 1995).

The last component of Sterling's (1993) definition of social organisation, the mating system, has been more difficult to assess. This is due to several factors: poor observational conditions at night, the cryptic behaviour of most nocturnal primate species, the use of more subtle forms of communications, such as olfaction (Charles-Dominique, 1978; Clark, 1985), which allow animals to interact indirectly, and the more dispersed behaviour of animals in space and time (Sterling *et al.*, 2000; Sterling and Richard, 1995). Thus, for the mating system of nocturnal primate species to be assessed more accurately, the use of molecular genetics, such as paternity testing, combined with long-term behavioural data, is necessary. Nevertheless, some assumptions, based on a combination of spatial and social patterns observed and behavioural data collected during times of oestrous, can be made with regards to the mating system exhibited by a species (Bearder and Martin, 1980; Bearder, 1987; Harcourt and Nash, 1986; Muller, 1998; Radespiel, 2000). Despite the increase in studies conducted on prosimian societies and the advancement of radio-tracking technology, our knowledge on the social organisation of lorisines is limited to relatively few studies (Table 1.2), only three of which used radio-telemetry to investigate ranging patterns (*Nycticebus coucang*: Wiens and Zitzmann, 2003a, b;

Nycticebus pygmaeus: Streicher, 2004 and Starr, 2007 (pers. comm..); *Loris lydekkerianus malabaricus*: Kar Gupta, 2007).

Table 1.2. Spatial and social systems of lorisines based on five long-term studies in the wild, three of which used radio-telemetry (*Loris lydekkerianus malabaricus*, *Nycticebus nycticebus coucang* and *Nycticebus pygmaeus*).

Taxa	Social system	Spatial system	Source
L. l. lydekkerianus	Gregarious and dispersed	Multimale/ multifemale	Nekaris, 2003a Radakrishna, 2002
L. l. malabaricus	Dispersed	Unimale/ unifemale	Kar Gupta and Nash, 2001
Nycticebus coucang coucang	? but 3% social interactions	Unimale/ unifemale	Wiens & Zitzmann 2003a, 2003b
N. pygmaeus	?	?	Streicher, 2004
N. pygmaeus	Gregarious and dispersed?	Multimale/ multifemale?	Starr, pers.comm. 2007

No long-term studies have been conducted on any of the Sri Lankan slender loris taxa and the little information available on aspects of the social organisations of *Loris tardigradus tardigradus* is mostly anecdotal. Phillips (1935) reports that it was mostly found alone or in pairs and that there was no evidence of reproductive seasonality. Petter and Hladik (1970) suggested a solitary lifestyle on the basis that they were never seen together or at distances of less than 100 metres apart, that they rarely used the loud call, which they interpreted as having a territorial context, and that their reproduction was highly seasonal (Manley, 1966). During more recent surveys in MPFR though, lorises were reported to be in groups of up to three animals, usually consisting of adults and their youngsters (Nekaris and Jayewardene, 2003).

Studies on sociality of slender lorises are limited in comparison to other prosimians. Long-term studies on *L. l. lydekkerianus* revealed that animals spent 38% of their

active time being social (within 30 metres of another individual), with affiliative and neutral interactions being the most common (Nekaris, 2000, 2006; Nekaris and Bearder, 2007). Most of these interactions were between males and between males and females, and animals that shared sleeping sites. Lorises were gregarious not only at the sleeping site but also throughout the night. *L. l. malabaricus* also showed high levels of sociality as they spent 40% of their time together, but a widely varying degree of cohesiveness between adult pairs sharing a home range (Kar Gupta, 2007). The mating system has not been described with certitude in either case due to the lack of molecular data to support spatial and social patterns observed. Nevertheless, in the case of *L. l. lydekkerianus*, the mating system was described as polygynandry (Nekaris, 2000; Radakrishna, 2001), and in the case of *L. l. malabaricus*, Kar Gupta (2007) proposes a more flexible approach to mating by male lorises, in that they switch from a polygynous to a more monogamous mating system once they have settled into a unimale-unifemale spatial system.

1.4. BACKGROUND TO THE CURRENT STUDY

There is an obvious lack of information available on *L. t. tardigradus*, and in particular, its behavioural and social ecology. This lack of long-term research on Sri Lankan slender lorises may be attributed to several factors: lack of national and local interest in the species, belief that the species is widespread throughout the country, as a result of all forms being lumped as one species, and a civil war, which has had a negative effect on all forms of research on Sri Lankan wildlife. The difficulty in studying these primates at night, particularly the rainforest and montane forms, also meant that the use of radio-tracking was inevitable. The difficulty in obtaining permits to bring in radio-tracking equipment into a country at war, and the difficult and

lengthy procedures imposed by the Department of Wildlife Conservation and the Telecommunications Regulatory Commission of Sri Lanka made this project a challenging task from the beginning. Nevertheless, permits were eventually obtained to conduct a one-year radio-tracking study on slender lorises at MPFR, and during that time, data on ranging behaviour, social behaviour, habitat and microhabitat use, and activity, could be collected on 21 animals, including 18 adult and subadults (nine males and nine females) and three non-collared juveniles. Despite the ability to track and follow animals, the difficulty in observing the animals, as a result of their cryptic behaviour and the dense rainforest environment, meant that relatively little data could be collected on certain aspects of their behaviour such as mating, mother-infant interactions and social behaviour at the sleeping site.

The rise of modern behavioural ecology and socio-biology have rendered descriptive 'natural history' studies obsolete, replaced by more empirical studies that test specific hypotheses about an animal's behaviour or ecology. In this study I test specific hypotheses about the social organisation and ecology of *L. t. tardigradus*, the results of which appear herein, but I also conducted this research in the hope that it would provide a quantitative natural history of this little-studied primate. The value of a descriptive account of the behaviour and ecology of this species is warranted because of the absence of any other long-term field data on *L. t. tardigradus* and by the general paucity of long-term field data for most species of lorises. In addition, in spite of the fact that I have spent over 6000 hours in close contact with the slender lorises at MPFR, this is in a sense a preliminary study, in that it lacks comparative data from other sites at which the species' ecology is clearly different from that at MPFR. However, this does not reduce the importance of the findings revealed in this study. Instead, this study may be seen as a first stepping stone for future comparative

research, which will result in more empirical studies testing specific hypotheses about the behavioural ecology and socio-biology of *L. t. tardigradus*.

The importance of this study is evident in an additional aspect. As I was writing up my thesis I was lucky enough to act as advisor for a large-scale conservation project of *L. t. tardigradus* conducted by the Zoological Society of London. Much of the advice and background information given for the research proposal, implementation plans, meta-population analysis and conservation goals for the red slender loris conservation project, were based on the information gained from this study. This study thus serves two important purposes: it provides the foundation for future comparative studies on the socio-ecology and behavioural ecology of slender lorises in Sri Lanka, and by evaluating the social, ecological and behavioural plasticity of lorises at MPFR, more effective conservation strategies can be applied for this endangered and little-studied strepsirrhine.

1.5. STRUCTURE OF THIS THESIS

I structure this thesis in a traditional format. Following this introduction, I describe the methods then present the results section, which starts with a descriptive section providing the reader with background information on MPFR and lorises at MPFR. It includes a description of the study site: extent, floristic composition, mammal diversity; and the study population: population density, population structure, morphometrics, reproductive characteristics, behavioural ethogram, and activity budget and activity rhythms. This is followed by the results on ranging behaviour, social behaviour, habitat and microhabitat use and the influence of abiotic factors on behaviour. Although I structure the discussion around the four aims of the study,

information from different parts of the results section are used throughout, as each aspect presented in this thesis contributes in some way or another to each of the four sections in the discussion. I conclude this thesis by proposing avenues for future research based on questions raised from this study. Additionally I present in Appendix 4 an unpublished paper evaluating different methods of estimating home range size, which I touch upon in the methods section but present in more detail in this appendix.

CHAPTER 2 STUDY AREA AND METHODS

2.1. THE RESEARCH TEAM

This study was conducted in two major parts: one from October 2004 to August 2005 consisting of a pilot study, nocturnal and diurnal surveys and vegetation surveys, and the second one, between August 2005 and August 2006 consisting of the radio-tracking and behavioural study. Throughout the two study periods I had one field assistant (Adin Beresford) who assisted me in every part of the research project. In the first six months of the study, a local villager (K.K.Nallaka), worked as our forest guide to help us find forest paths, map the forest, and avoid trap guns and live wires. Beresford and I conducted the first five months (August to December) of the radio-tracking study, and in January 2006 I obtained the additional assistance of Karl Davey and Megan Collins to radio-track an increasing number of lorises, for the months of January, February and March. In April, Collins was replaced by Robert Davies, a postgraduate student from UCL, who assisted Beresford, Davey and me with the radio-tracking regime until the beginning of July. Davies also assisted me in the recording and digitising of vocalisations, which he used for his master's thesis (Davies, 2007).

Inter-observer reliability was tested by researchers collecting data simultaneously upon sighting an animal. Each researcher would be allowed to collect data independently once inter-observer reliability tests were satisfactory. In addition, regular tests were conducted throughout the study period to ensure consistency in the way observers measured behaviour. These tests consisted in having each researcher measure the same sample of behaviour on three occasions based on video-taped behaviour (Martin and Bateson, 2001).

2.1. THE STUDY SITE

MPFR (6°02 N and 80°36 E) is a moist semi evergreen forests (also referred to as moist monsoonal forest) with an estimated annual rainfall of 1100-1400 millimetres. It is situated at the southern end of the Intermediate Zone, between the Wet and Dry climatic Zones and belongs to the Kamburupitiya and Thiyagoda secretariat divisions of Matara District. It is surrounded by village settlements, large networks of paddy fields and three roads, thus isolating it from other forest patches (Figure 2.1).

Figure 2.1. Map of Sri Lanka and MPFR. The map of Sri Lanka shows forest cover (in green) and a rough delineation of the three main climatic zones (the Wet Zone, the Dry Zone and the Intermediate Zone) based on annual rainfall. MPFR is one of the very small forest patches of moist monsoon forest in the Intermediate Zone and is shown on the right in textured green. It is surrounded by urban settlements (in yellow), large networks of paddy fields (in plain green) and roads (in red).

No exact records of the current extent of the forest are available, but earlier Forest Department records show the following estimates: 30 hectares of ridge forest; 12.5 hectares of closed canopy forest; 141 hectares of exploited forest; 90 hectares of scrubland; 96 hectares of forest plantations and 51 hectares of agricultural land, totalling an area of approximately 420 hectares, with forest plantations and agricultural land included, and 273 hectares of just forest and scrubland. Being a proposed forest reserve, MPFR is only partly protected by the Forest Department and is regularly used by villagers for fuel wood, liquor production, medicines and rice cultivation (pers. obs., Nekaris *et al.*, 2005). The forest is surrounded by pine forest plantations owned by FreeLanka, a private company which owns estates across the southern province, and which act as a buffer zone to protect the forest from further encroachment and degradation (Ashton *et al.*, 1997) but also provide buffer communities with a monthly income from resin tapping. Other forest plantations include rubber and are much smaller and owned by families living on the forest edge. Rubber plantations form one of the other main sources of income in rural areas of Southern Sri Lanka (Herath and Takeya, 2002). Approximately 65% of rubber plantations in Sri Lanka are less than 20 hectares in size and are mostly owned by smallholders (Ali *et al.*, 1997) as is the case in MPFR (Figure 2.2).

Figure 2.2. Small rubber plantation belonging to the Ariyasiri family on the edge of MPFR.

Rice paddies, which are scattered around and across the forest, form a regular source of food rather than income but are often abandoned as a result of wild boars destroying the crops, or flooding. What remains are grazing fields for livestock, which create wide gaps within the forest (Figure 2.3).

Figure 2.3. Abandoned paddy field used as a grazing field and fragmenting MPFR.

The climate at MPFR is typical of the Wet Zone in that it mostly rains throughout the year and temperatures are cooler than Dry Zone forests. Data on temperature and rainfall were obtained from the records of the Andapana Estate, of Maturata

Plantations Ltd, situated 2.3 kilometres from MPFR. Figure 2.4 shows the trend in total monthly rainfall and average monthly temperature obtained from averaging data collected between 1998 and 2007.

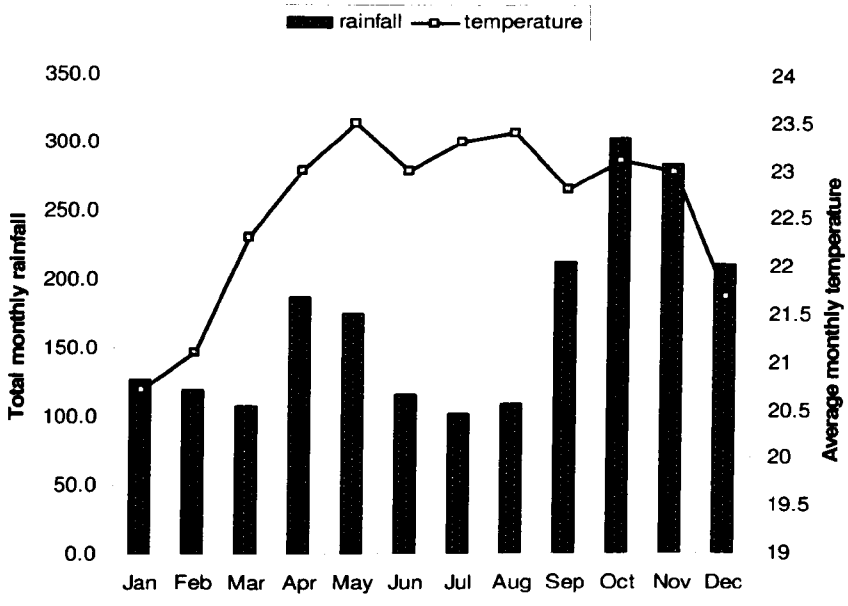


Figure 2.4. Average total rainfall and average monthly temperature for the years between 1998 and 2007.

2.3. PREPARATION OF THE STUDY SITE

Within MPFR, the study area covered approximately 85 hectares, of which 24 hectares consisted of rice paddies and pine forest plantations, within the forested area and along the forest edge (Figure 2.5). No recent maps of MPFR at the required scale were available at the start of the study, so a map (Figure 2.5) was constructed using GPS Utility and ArcMap to plot satellite coordinates taken using a Magellan eXplorist 210 handheld GPS unit (Global Positioning System unit), along the forest edge, the village paths, marked trails, dirt roads, paddy fields and pine forest plantations. In areas where satellite points could not be taken, the next point (of the path, edge, etc)

would be taken by using a tape measure and a compass. Upon my return from the field I was able to obtain a satellite map of MPFR with good resolution using Google Earth and could verify the accuracy with which I had mapped the forest edge, pine forest plantations and paddy fields. The village paths could not be seen on the satellite map as the forest canopy covered them.

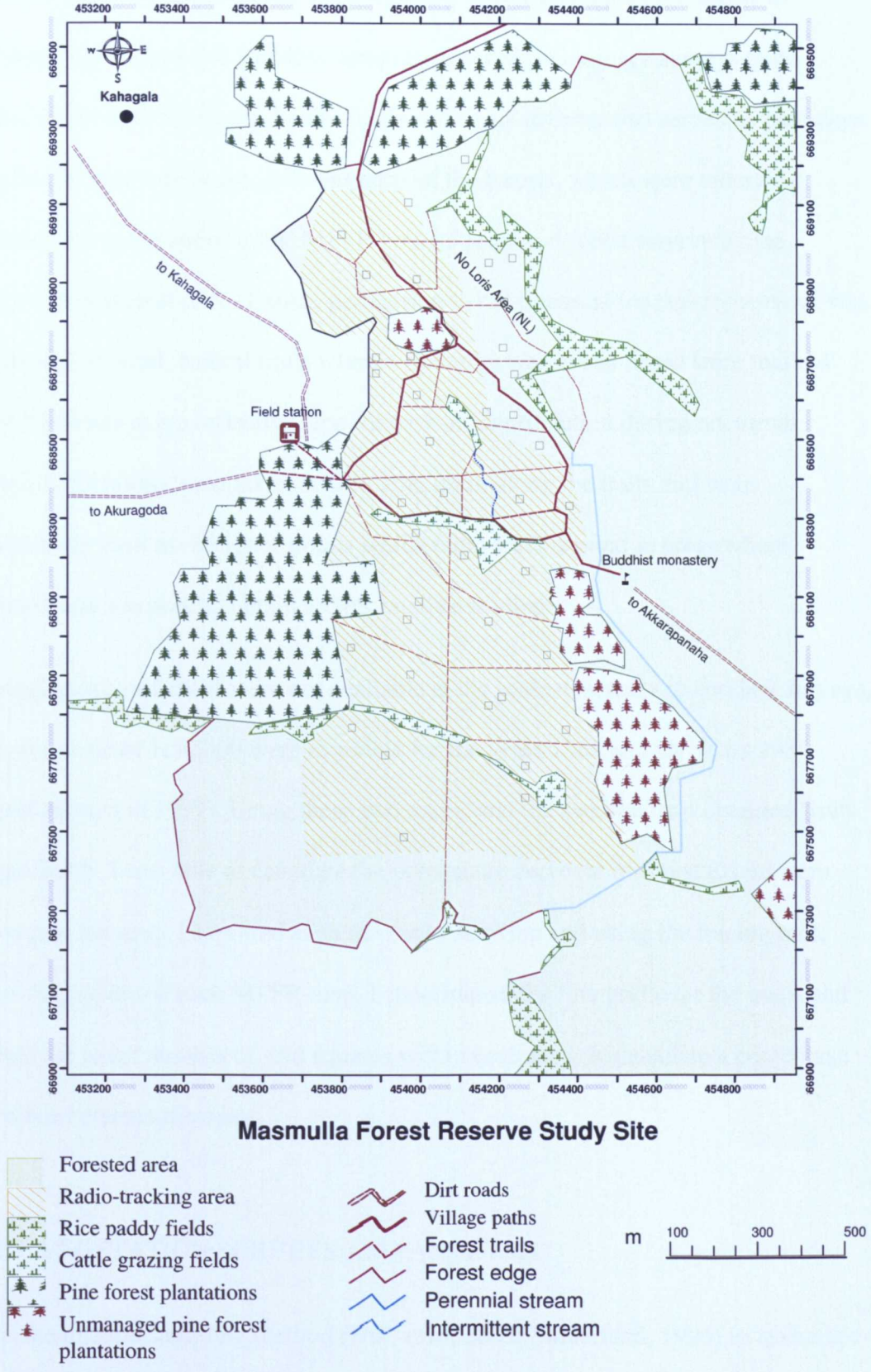


Figure 2.5. Study site within MPFR. The area in green represents natural forest whilst areas in white represent non-forested areas (i.e. human settlements). Grey squares = 10m x 10m vegetation quadrats (not to scale). SS = study site areas. NL = No Loris area. NST = Nth-Sth Trail; VP = Village Path 1, 2 and 3) SP = Stream Path.

Four village paths, two of which were regularly used by villagers for access to neighbouring villages and Buddhist temples, allowed preliminary surveys to be conducted through the forest. Paddy fields and small streams also served as pathways, and allowed access between different parts of the forests, which were otherwise inaccessible via the major trails. MPFR being a proposed forest reserve by the Forestry Department of Sri Lanka, permission to cut transects for density surveys was not granted. Instead, natural trails where vegetation was not as dense were marked every 20 metres using reflective tape for ease of identification during nocturnal surveys. GPS points were taken at each 20m mark along the trails and were subsequently used as reference points whilst radio-tracking and in areas where reception was too poor to obtain a GPS satellite reading.

Although maps of MPFR were not available at the scale necessary to conduct surveys, maps at a scale of 1:50,000 were available for the years 1968 and the years 1985 (revised edition in 1999). Using these two maps, and the satellite map obtained from Google Earth, I was able to calculate the percentage decrease of forest extent from one map to the next. I exported each map onto ArcMap and using the tracing tool, traced the outside of each MPFR map. I superimposed a fine grid over the maps and counted the exact number of grid squares within each map, to calculate a percentage difference between the maps.

2.4. VEGETATION SURVEYS AND ANALYSIS

I used the quadrat sampling method (Hill, *et al.* 2005; Sutherland, 1996) to assess the floristic composition and richness of the forest stand encompassing areas SS1, SS2 and NL (Figure 2.5). Plants were identified by a local villager (Ariyasiri) whose

family remains one of the few in the village to use plants for medicine and who possesses extensive knowledge of this tradition. I had a proportion of the samples (80%) identified by officers of the Department of Forestry and botanists of the University of Peradeniya Botanical Gardens to ensure that identification was correctly made.

Preliminary nocturnal surveys (see Section 2.5.1) and a previous study on slender loris density at MPFR (Nekaris *et al.*, 2005) revealed an uneven distribution of lorises across the study site, with some areas having a higher density of lorises than others and one area yielding no loris sightings during the two years in the field . In some areas, these density patterns appeared to coincide with the distribution of two plant species, a small tree species, which appeared to dominate much of the forest, *Humboldtia laurifolia* (Leguminosae) and a bamboo shrub, *Ochlandra stridula*, which dominated in areas where *H. laurifolia* was less extensive. The former of these two plant species was identified in a previous study as being associated with high slender loris density (Nekaris *et al.*, 2005). Thus, vegetation surveys were conducted in the area where no lorises had been sighted and in areas where lorises had been sighted and/or radio-tracked, which was further divided into two areas based on presence/absence of *H. laurifolia* and *O. stridula.*

The floristic composition within each of these three forest stands was assessed by randomly placing between eight and ten quadrats measuring 10m x 10m, resulting in a total of 37 quadrats (Figure 2.5). Within each quadrat, trees with a circumference at breast height (CBH, measured at approximately 130 centimetres above ground) above 10 centimetres were identified and counted. For buttressed trees the diameter was taken just above the buttress. For trees with multiple stems the total CBH was calculated as the sum of all individual CBH values (of each stem). The following

parameters were calculated for each of the three forest stands: species richness, number of families and genera, Shannon-Weiner's index of diversity, Simpson's concentration of dominance, Sorensen's index of similarity, stand density and basal area. A description of each parameter is given in Appendix 1. This method follows Mueller-Dombois and Ellenberg (1974) and others (e.g. Sundriyal *et al.*, 1994; Pandey and Shukla, 2003; and Bhuyan *et al.*, 2003). The dominant tree species within each stand type were determined from the Importance Value Index (IVI) (Curtis and McIntosh, 1950) of each tree species, which was calculated as the sum of the relative density (rD), relative basal area (rB), and relative frequency of occurrence (rF) in each quadrat (Pascal and Pelissier, 1996). Percentage cover of the bamboo *O. stridula* was estimated using the Braun-Blanquet scale (Kent and Coker, 1992). To assess floristic composition within home gardens, five home gardens on forest edge were visited to identify tree species and estimate height. In addition, shrub species growing in regenerating forest plantations were identified. Forest plantations (rubber and pine) stands consisted only of trees belonging to the species in question (pine or rubber), of near equal heights and spaced at regular distances with no undergrowth or connectivity in between. Thus, vegetation sampling was not conducted in such stands.

2.5. ANIMAL SURVEYS AND LORIS TRAPPING REGIME

2.5.1. Nocturnal and diurnal surveys

We conducted 113 nocturnal and 63 diurnal surveys for a period of five months between October 2004 and May 2005 in an area measuring approximately 140 hectares and depicted in Figure 2.5. At least one assistant (Nallaka and/orBeresford) and I, conducted diurnal surveys opportunistically between 07.00 and 09.00 (after

nocturnal surveys) and between 16.00 and 18.00 (before nocturnal surveys), along three village paths in SS2, a forest trail in area SS1, and a village path running along the perennial stream and pine forest plantation in SS1 (Figure 2.5), at a speed of 0.5 - 1km/hr. I collected two sets of data to obtain an estimate of abundance (Davies, 2002): the total length of the trail surveyed (length of trail multiplied by the number of times it was walked) (Table 2.1) and the total number of primate groups and individuals (for all other species) encountered, and express abundance as the number of groups/individuals encountered per kilometre walked.

Table 2.1. Characteristics of paths walked for nocturnal surveys and diurnal surveys, including the length of the path (in meters), the number of times each path was walked and the total surveyed length of each path (in kilometres). VP (1, 2 and 3) = village paths (1, 2 and 3); NST = North to South Trail; SP = Stream Path.

Surveyed paths		**VP1**	**VP2**	**VP3**	**NST**	**SP**
Length of paths (m)		870	690	600	800	1200
Nocturnal surveys	Number of times path walked	130	98	91	83	50
	Total length of path walked (km)	113.0	58.8	54.6	66.4	60.0
Diurnal surveys	Number of times path walked	28	34	16	22	30
	Total length of path walked (km)	24.4	23.5	9.6	17.6	36.0

We conducted systematic nocturnal surveys between 18.00 and 7.00, four to five times a week and during all moon phases so that each path was walked during each moon phase. The night was recorded as being either dark if the moon phase was new or crescent, or bright, if the moon was full or gibbous. Surveys were carried out along

the same five paths used for diurnal surveys and also along a dirt road running from the Buddhist monastery and covering an area outside the main study site (Figure 2.5). Slender loris abundance was estimated as described above for diurnal primates. Table 2.2 summarises the nocturnal survey efforts based on a total of 106 nights conducted between October 2004 and May 2005. Sightings of other mammal species during nocturnal surveys also were recorded.

Table 2.2. Summary of nocturnal survey efforts for the 5 month period spanning from October 2004 to March 2005 and excluding the month of November.

Survey Efforts	**Min**	**Max**	**Mode**	**Mean**	**SD**
Nights/month	11.0	25.0	19.0	19.7	1.3
Hours/night	2.0	12.0	6.0	7.5	2.8

Nocturnal surveys were conducted using hand-held lights (MagLight) and headlamps (Petzl, MegaZoom), operated with a halogen bulb and powered by rechargeable batteries. Headlamps were fitted with red filters to minimize disturbance to slender lorises and other animals present in the forest (Barett, 1984; Nekaris, 2000). Slender lorises possess a reflective layer at the back of the retina, called the *tapetum lucidum*. When using white torch light this results in a distinctive bright orange reflection of their eye shine, thus allowing the animals to be spotted in the night. The use of a red filter had the effect of turning eye-shines of other arboreal mammals, such as civets or cats, orange instead of their natural greenish-blue or yellow eye shine. This could result in those eye shines being confused for that of a loris, particularly if the animal was high up in the trees, partly hidden, far away, or spotted very briefly. Thus, when in doubt, one observer would shine a white light on the animal to reveal the true

colour of the eye-shine. This also often had the effect of making the animal move, which aided in distinguishing it from a loris. We also used white torch light in areas where detection distance may have been diminished as a result of dense canopy. Whenever an animal was spotted, we would switch to red light so that the animal would not flee and its normal behaviour could be recorded.

2.5.2. Trapping regime

As from May 2005 a trapping regime using twelve modified tree shrew traps was conducted in an area of high slender loris abundance (SS2). To increase chances of catching a loris, camouflaged traps were placed in specific trees where lorises had been sighted at least twice during nocturnal surveys, and at an average height of 3m (this being the average height recorded by Nekaris *et al.*, 2005). We also covered the traps in treacle to attract ants and other insects and baited them with banana and peanut butter. Unfortunately, five of the traps were stolen within two weeks of being placed. Ordering more traps proved uneconomical, so the trapping regime continued for a further three months with the remaining seven traps. Traps were checked three times a night (at the start of the night, at around midnight and once just before dawn) and the bait changed every day. Despite the baited traps being placed on branches known to be used by lorises, no lorises were ever caught. I conducted a similar trapping regime at a different forest in Sri Lanka in a pilot study (Bernede, 2003), and also caught no lorises then. Failure to catch animals was speculated to be the result of low loris densities at that site, unlike MPFR, and the less sensitive release mechanism of the traps used in that study. However, the failure at MPFR, despite using better traps and having traps placed in areas of high slender loris density, suggests that, like other lorisines (pottos: Pimley, 2002; slow lorises: Barrett, 1984; Wiens, 2002),

lorises may simply be trap-shy, resulting in extremely low catch rates (e.g. catch rate of 1/1081 trap nights for *Nycticebus coucang*: Wiens, 2002).

Previous studies on slender lorises have found that catching slender lorises by hand was a more efficient method (Radakrishna, 2001; Nekaris, 2000). This may have been facilitated by the fact that the habitat type consisted primarily of scrub forest, rather than rainforest as in MPFR, making it relatively easier to isolate the animal on a small tree and subsequently catch it by climbing the tree (Kar Gupta, 2007) or bringing the branch down (Nekaris, 2000). Trees at MPFR were relatively higher and overall, the forest denser, resulting in lorises always having an escape route. The relatively fast speed at which the red lorises move (see Nekaris and Stevens, 2005) also made it extremely difficult to approach and catch, as one would with a relatively slower species. Nevertheless, catching the animals by hand proved to be the most efficient strategy once animals had become habituated and did not run away when approached by myself and my assistant (Beresford). The opportunity to catch a loris presented itself when the animal in question came down to a height below two metres and few escape routes were available. At that time it was possible to move swiftly towards the animal and catch it using a small towel to cover its head, thus preventing it from running away. After the first capture by hand on the 1st of August 2005, we were able to catch an animal on average every fortnight. We ceased to catch additional animals two months prior to the end of the study. Catching the same animal twice proved impossible but all animals eventually lost their radio-collars, by either slipping them over their heads as they had been fitted loosely enough, or by another animal chewing through it, or through wear and tear. All collars were subsequently recovered. Once caught, the loris was wrapped in a towel, which created a dark environment, and carried back to the field station.

2.6. DATA COLLECTION AND ANALYSIS

2.6.1. Loris morphology and physiology

Once at the field station, morphological measurements and descriptions of physical appearance and condition were made according to a standard compiled by Schulze (2004) (see Appendix 2 for modified morphological recording sheet). A total of 15 morphometric variables were measured. Measurements were taken to the nearest millimetre using manual callipers and body weights measured using a 300 gram Pesola scale. Animals were weighed in a black cotton bag that could be safely attached to the scale. Testis volume was calculated using measurements for testis length and width of each testis and using the formula for the volume of a spherical ellipsoid: (π* testis length* (testis width^2)/6) (Groves and Harding, 2003). Reproductive condition of females was determined by the appearance of the vulva (closed and pale during non-oestrous periods, swollen and red at the onset of oestrous or open and pink during oestrous). Pregnancy could be detected by gently palpating the lower abdomen, whilst swollen nipples characterised lactating females.

Lorises were categorised into the following age classes: infant, juvenile, sub-adult and adult. The criteria used to define these categories come from various studies conducted on Lorisidae (Rasmussen, 1986; Schulze and Meier, 1995; Nekaris, 2000; Fitch-Snyder and Ehrlick, 2003; Radakrishna and Singh, 2004).

An animal was said to be an infant if it was carried by the mother and parked, whilst a juvenile was an animal that was not parked and showed independence of movements but was smaller in size than a subadult (bigger head to body ratio) (Rasmussen, 1986; Schulze and Meier, 1995; Fitch-Snyder and Ehrlick, 2003).

In the case of females, signs of sexual maturity and thus of having reached adulthood include signs of primi- or multiparity (e.g. elongated nipples or if female is seen carrying infant) and signs of oestrous (swollen, turgid and reddened vulva; males pursuing female in an attempt to mate with her) (Schulze and Meier, 1995). Radakrishna and Singh (2004) point out that signs of sexual development (a subadult becoming sexually mature) were accompanied by changes in ranging patterns as females migrate from their natal home range. This criteria is used to help categorise one of the females FG as a subadult, along with evidence from other age defining characteristics.

In ageing animals more white hairs appear on the face and to some extent on the body, giving the fur a greyish to whitish appearance. In addition, grey and dark pigmentation appears on the otherwise yellowish, pinkish ears of young slender lorises. Thus, an animal with pink or yellow ears and without any grey or dark pigmentation is most likely young. This latter criteria however was not conclusive on its own and could only be used to support a judgement based on previously described criteria (weight, size, description of genitalia and behaviour). On the other hand, in a study conducted on *L. l. malabaricus*, Kar Gupta (2007) was able to correlate pigmentation to age classes with juveniles having bright yellow ears, young adults having light yellow pigmentation and older adults having dark greyish yellow pigmentation, which supports the observations made in this study (at least with regards to the dark pigmentation seen in older animals) and observations made on captive *L. l. nordicus* (Schulze and Meier, 1995). The distinction between subadults and young adults, however, could not be made using pigmentation patterns alone, and remains a difficult one to make without additional supporting evidence. Males were easily distinguished between adults and subadults as subadults lack scrotal

pigmentation (Schulze and Meier, 1995). In this study none of the caught males were subadults as all showed scrotal pigmentation. Based on these definitions I include in Appendix 3 a table showing how I categorised each individual into a particular age class.

I used a long-established protocol for taking rapid morphological measurements without the need for anaesthesia (Nekaris and Jaffe 2007). At the field station, this method resulted in an average time taken to collect morphological data and fit the radio-collar, of 41 minutes (± 10). This resulted, on average, in a total time of 60 minutes (± 18) from the moment the animal was caught to the moment it was released (excluding animals that were examined at the catch site and animals that were not collared) (Appendix 3). As animals were examined for relatively short periods of time, we did not have the opportunity to collect faeces

Once measurements were taken, a radio transmitter consisting of a TW-4 button cell tag transmitter (Biotrack Ltd, Dorset, U.K.) attached to a rubber-coated plastic collar, and weighing a total of 6g was fitted around the animal's neck, ensuring that the collar was loose enough that it could easily move. The battery of each collar could last up to six months and detection range varied between 150 metres and 300 metres (depending on weather conditions, canopy density and relief). Once the collar was fitted and all measurements taken, the animal would be transported back to the catch site for release and left alone for the rest of the night. Each radio-collar had its own frequency allowing the radiolocation of the animal to be detected using a TR-4 receiver (frequency range 230.000 – 230.990 MHz) (Telonics Inc.) and a flexible 3-element Yagi antenna (Biotrack Ltd, Dorset, U.K.). Radio-collars were not placed on juveniles as they weighed 75 grams or less (Appendix 3). Instead, a coloured plastic bird band with an inner diameter of eight to nine millimetres was placed around the

animal's ankle. This type of bird ring consists of a rolled up flat elastic tape that allows the spreading of the ring (Appendix 3) and does not inhibit movement, or in the case of juveniles, growth. This type of bird band has been used on slender lorises in captivity and was carried by the animals for years without any problems (Schulze, 2004.). They also were used on pygmy slow lorises at the Endangered Primate Rescue Center, Vietnam, and no problems were observed (U. Streicher, unpublished, from Schulze, 2004).

Statistical analysis: In addition to statistics used to describe the morphology and physiology of the 21 slender lorises caught, I tested for inter-sexual differences in body weight and total body length using the student t-test (data met the assumptions of normality). To give the reader an indication of the variability of original data points I present the mean $\pm$ SD as a descriptive statistic. When inferential statistics are used and graphs are presented to supplement statistical tests, I draw error bars (2SEs or t x SE when sample size is small) around the mean values, to show the range within which the true mean or difference between means may be found (Streiner, 1996; *Cumming et al.*, 2007). Tests are two-tailed and significance levels set at $p < 0.05$. P-values between 0.05 and 0.06 are interpreted as tendency towards significance.

2.6.2. Activity rhythms and general activity budget

I aimed to assess the three following aspects of loris activity based on a data set of 13 radio-collared individuals (seven females and six males):

1. Activity rhythms across a 13hournight (between 18.00 and 07.00) to assess the percentage of time lorises were active in each hour of the night, including time at which activity started and ended.

2. Monthly activity rhythms across the year to assess the percentage of time lorises were active in each month of the year and investigate potential effect of monthly changes in abiotic factors.

3. General activity budget to assess the percentage of time lorises allocated to different behavioural activities.

To assess the daily and monthly activity rhythms of lorises at MPFR, I recorded whether an animal was 'moving' and thus being active, or 'stationary' and thus being inactive. An animal was recorded as being 'stationary' (or 'inactive') if it exhibited the following behaviours: 'sleep/rest', 'groom' or 'exploring without moving'. The category 'moving' (or 'active') was recorded whenever the animal was observed moving, whether during foraging, exploring or travelling (see Section 3.3.1 for a detailed behavioural ethogram. I use in this thesis the same terms used in previous slender loris ethograms (Nekaris, 2000; Radakrishna and Singh, 2002)). When the animal was not visible I would listen to the strength and amplitude of the radio signal. Animals would be considered as moving if signal amplitude from the transmitter was fluctuating or if the animal's location had changed since the last radio location. My assistants and I were able to associate certain behaviours with signal fluctuations as we watched the animals whilst listening to the signal and this helped identify whether the animal was moving or stationary, even when out of view. For example, when an animal was grooming, the signal fluctuated slightly as the animal moved its head up and down or back and forth. Travelling resulted in the signal being steady but becoming weaker quite rapidly as the animal moved away. When the animal rapidly moved up and down lianas the signal would drastically drop then pick up in amplitude again. When foraging in dense bushes or moving between bushes, the signal fluctuated a lot as the antenna would be temporarily blocked. When the animal was

not moving (whilst resting, sleeping or exploring without moving), the signal fluctuated minimally or not at all (Table 2.3).

Table 2.3. Sampled behaviours and radio-signal cues used to differentiate 'stationary' from 'moving' to describe activity rhythms.

Activity Category (radio-signal clue when animal not visible)	Behavioural Category	Behavioural Category Description
STATIONARY (INACTIVE) Radio-signal steady for more than 1 minute. No or few fluctuations in signal amplitude.	Sleep / rest	Sleep: animal curled up in a ball, eyes closed. Rest: animal sitting with eyes closed or closing. Not looking around or listening.
	Exploring without moving	Animal in a standing/sitting position, not moving but scanning surroundings (looking around, listening and being aware).
	Grooming:	Auto-grooming: self grooming. Allo-grooming: one grooming another or both grooming each other.
MOVING (ACTIVE) Radio-signal fluctuating for more than 1 minute. Fluctuations pronounced due to antenna moving, animal moving up and down, and moving through foliage.	Foraging	Animal actively searching for food.
	Exploring whilst moving	Animal moving, often slowly, regularly stopping, and scanning surroundings.
	Travelling	Animal moving fast in one direction covering distances > 10 m without stopping.

I tested the reliability of this method by watching an animal and recording its behaviour whilst my assistant would listen to the signal without watching the animal and record whether it was active or inactive based on fluctuations. In addition, we tested this during light rain to ensure that this would not cause the signal to fluctuate even though the animal was not moving. After a period of about one month of practice, we were able to distinguish whether the animal was moving or stationary from the radio-signal for over 97 percent of cases. Whilst not a substitute of direct observations, or collars that are specifically designed to record activity, this method

allowed me to collect data on activity without necessarily seeing the animal. In cases where the animal was not visible and the signal not detectable I would record that sample point as 'not visible'. I stopped the recording session when I could no longer see the animal or detect the signal after ten minutes.

To describe the hourly activity rhythms of lorises, I divided each night into 13 hourly intervals (between 18.00 and 07.00) and recorded the percentage activity in each time interval. I collected an activity/inactivity point every five minutes and calculated an average for each time interval and each animal. I visited each animal an average of 38.3 ($\pm$ 14.2) times per interval. The same method was used to describe the monthly activity rhythms of lorises between August 2005 and June 2006, but calculating an average for each animal, for each month.

In addition to describing the hourly and monthly activity rhythms of lorises, I aimed to describe how much time lorises allocated to the following broad behavioural categories: sleeping/resting, grooming, foraging, exploring, travelling and other and tested whether activity budgets varied between sexes and between months. When the animal was foraging and/or feeding, every attempt was made to see the item eaten and was placed into one of the following categories: insect, fruit, flower or gum.

When the animal was obscured from view I waited 10 seconds after the five minute interval to record its behaviour (Boinski, 1988; Fragaszy *et al.*, 1992). If after 10 seconds the animal was still obscured from view I recorded the sampling point as 'not visible'. Animals would generally be visible again within ten minutes, in which case I would continue the recording session and record sample points as 'not visible'. If the animal was lost or out of view for any longer than 10 minutes, I would stop the recording session and start a new one, once I identified the focal animal again.

Statistical analysis: All the statistics used for this section are descriptive. Values are given as means ± SD to show spread of hourly and monthly activity scores.

2.6.3. Radio-tracking regime and ranging data collection

With radio-telemetric data I aimed to assess the three following aspects of loris ranging behaviour:

1. Home range size and core area size of radio-collared lorises using the best possible estimating method.
2. Overlap of home range and core areas, between radio-collared individuals, both inter-sexually and intra-sexually.
3. Home range defendability.

In this thesis I define a home range using Burt's definition (1943:351) that forms the foundation of the general concept used today: "that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range". If all or part of the home range is defended (or can be defended) against other individuals of the same species, the defended area can then be termed, a territory (Morse, 1980; Maher and Lott, 1995). Thus, I do not refer to individual home ranges in this thesis as 'territories' until evidence for defendability has been shown.

We radio-tracked fifteen adults and two subadults between August 2005 and August 2006 (Table 2.4). However, only twelve adults and one subadult (female FG) had enough location fixes to conduct ranging analysis. Since the three caught juveniles were not radio-collared, location fixes were taken on an opportunistic basis when their

coloured bird band was visible. I allocated equal efforts to increasing the number of animals radio-collared and the number of fixes collected for each animal in order to obtain a representative sample of the existing population whilst also providing a reliable estimate of home range size for each individual (Millspaugh and Marzluff, 2001).

We were able to follow lorises through most parts of the forest and take location points using a Magellan GPS unit every five minutes. We conducted focal follows between 18.00 and 07.00 for a total of 1070 hours. Tracking periods ranged from one to 11 hours per night depending on circumstances (Mean = 6.5 hours $\pm$ 2.7 per night). We radio-tracked animals for an average of 20.7 $\pm$ 13.6 nights and an average of 603.1 $\pm$ 506.0 fixes were obtained per animal. Males Ma, MC and ML and female FR, were tracked for less than ten hours, and five lorises, FE, FB, MJ, MD and MT were tracked for the maximum possible period of six months (Table 2.4).

Table 2.4. Individuals caught at MPFR, the number of individuals radio-tracked, their sex and age, the number of hours they were tracked, the number of location points collected (at five minute intervals) and the months they were followed.

ID	Age-Sex	Tracking days	Location fixes	Sleeping site fixes	Months
FE	Adult Female	35	1168	50	Dec 05 – Jun 06
FF	Adult Female	15	327	10	Sep 05 -Nov 05
FB	Adult Female	38	1639	47	Dec 05 - May 06
FI	Adult Female	26	1057	29	Jan 06 - May 06
FG	Subadult Female	22	1059	19	Feb 06 – Jun 06
FK	Adult Female	25	691	15	Mar 06 - Jun 06
FM	Adult Female	15	346	7	Apr 06 – Jun 06
FR	Subadult Female	3	37	2	Jul 06 – Aug 06
FJ*	??	NA	72	0	Nov 05 - Dec 05
MJ	Adult Male	19	486	19	Aug 05 - Dec 05
MA	Adult Male	11	303	9	Aug 05 -Sep 05
Ma	Adult Male	4	89	3	Oct 05
MD	Adult Male	33	625	46	Aug 05 – Feb 06
MT	Adult Male	48	1525	48	Nov 05 – May 06
MC	Adult Male	3	55	3	Nov 05
MH	Adult Male	19	681	20	Mar 06 - Jun 06
MO	Adult Male	18	611	10	Apr 06 - Aug 06
ML	Adult Male	5	85	6	Apr 06 - May 06
J1	Juvenile Male	NA	NA	0	May 06 - Jun 06
J2	Juvenile Male	NA	NA	0	Jan 06
J3	Juvenile Male	NA	NA	3	Jun 06
21	9♀ 12♂	339	10767	346	Aug 05 – Aug 06

Bold **ID** represents those individuals without enough location fixes to produce a reliable estimate of home range size.
FJ* = female J was not caught but observed within the home range of other radio-collared lorises.

Whenever more than one radio-collared animal were present together, we took simultaneous location points for each animal every five minutes. This was made possible as one researcher would listen continuously for the radio-frequency signal of each of the animals (switching from one frequency to another took a few seconds), whilst the second researcher would observe the animals and collect behavioural data (whenever possible) and keep track of how far the second animal was, in

collaboration with the first researcher. Most times a third researcher would be present, in which case, he/she would take a GPS points of each animal's location as indicated by the first two researchers, at five minute intervals until the focal animal started moving away from the second one (or vice versa). If only two researchers were present, the first researcher would take the GPS points (although this was rare and most times three researchers were present).

Once the focal animal started moving away, the researchers would continue tracking it and would leave the second animal behind (the distance between the two was noted every five minutes though until they were 30 metres away). If the focal animal did not move but the second animal did, one or two researchers (the tracker and the person taking GPS points) would track the second animal until it was more than 30 metres away from the focal animal, at which point the tracking would be abandoned and researchers returned to the focal animal. The researcher in charge of collecting behavioural data would stay with the focal animal to continue collecting behavioural data.

I estimated the number of fixes needed to obtain a reliable range size estimate by plotting fixes against home range size until they reached an asymptote on the area-observation curve (e.g. Gese *et al.*, 1990) (Figure 2.6).

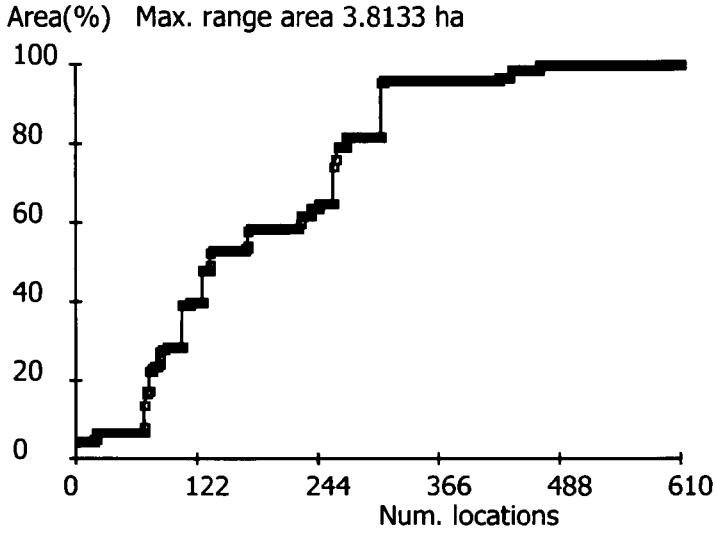


Figure 2.6. Incremental area-observation curve for one of the lorises, female FK, with the number of location fixes obtained plotted on the x-axis against the percentage of the maximum home range area obtained using MCP (100%).

Four of the radio-collared animals were not tracked long enough to allow an asymptote to be reached (e.g. Male ML, figure 2.7). Those were excluded from analysis. One sub adult female, FG, and an adult female, FB, also did not reach an asymptote but this was a result of dispersal rather than lack of fixes so they were kept in the sample for analyses (See Table 2.4).

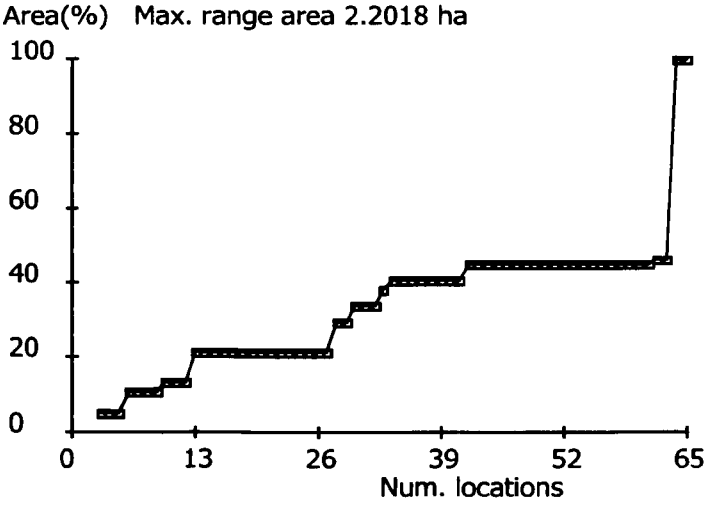


Figure 2.7. Area-observation curve for one of the males, ML, who was excluded from analysis, as the curve did not reach an asymptote.

Home range estimating methods: A wide choice of methods exist for estimating home range boundaries and internal cores (e.g. Dixon and Chapman, 1980; Anderson, 1982; Geissler and Fuller, 1985; Samuel and Garton, 1985; Kenward, 1987; Worton, 1989; 1995; Loehle, 1990). The earliest, most intuitive and still most commonly used method of estimating home range size is the Minimum Convex Polygon (MCP), which links up the outermost location points of a home range (MCP; Mohr, 1947, Seaman *et al.*, 1999). Another type of link distance method, known as 'between nearest neighbour' locations, can be used in cluster analysis to estimate size, shape and structure of home ranges (Kenward, 2001). Estimating home range size based on densities of location points is a method known as Kernel, and assesses an animal's probability of occurrence at each point in space (Worton, 1989, 1995; Seaman and Powell, 1996). It is typically reported as the minimum area that includes a fixed percentage of the estimated utility distribution volume (Millspaugh and Marzluff, 2001). This method, despite gaining in popularity for estimating home range characteristics (e.g. Taulman and Seaman, 2000; Dixson and Beier, 2002; Landa *et al.*, 1998; Te Wong *et al.*, 2003), has been criticised with regards to the smoothing factor used to calculate contours, in some cases resulting in overestimation of home range size as with the MCP method (e.g. Powell *et al.*, 1997).

I used the home range analysis package Ranges 7 (Kenward, 1987) to conduct home range analyses. To evaluate the method of home range analysis best suited to the ranging patterns exhibited by *Loris tardigradus tardigradus* in MPFR, I used four methods of home range analysis, two based on link distances between locations: the MCP and cluster analysis (Mohr, 1947; Kenward, 1987), and two based on densities of locations: Kernel Density Estimator (KDE) with the more widely used Least-squares cross-validation (LSCV)-calculated smoothing factor (h) value (h_{lscv}) and

KDE with h_{ref} multiplied by 0.75 to achieve a realistic estimate comparable across individuals. The bandwith *h* is a scaling factor, which controls the smoothness or roughness of a density estimate. It thus bears the danger of under- or over-smoothing (A full account of the principles underlying kernel smoothing may be found in Hastie and Tibshirani, 1990). The multiplier 0.75 was chosen by visually comparing home range contours obtained with different h_{ref} values (e.g. Worton, 1987, 1989; Pimley, 2002; Wauters *et al.* 2007).

Based on the results obtained using each of the four methods of home range analysis (Appendix 4) I decided to use the KDE method, and the MCP method. I defined an animal's total home range area and identified home range overlap based on estimates obtained using the KDE method with a probability of use of 0.95, thus excluding occasional excursions. Contours were fitted to locations using a smoothing factor *h* of 0.75. The number of fixes used to identify core area was identified in two ways:

1. By using a utilisation distribution curve of areas estimated with the MCP method, to assess (by eye) at which point the curve's steepness sharply decreases (Figure 2.8).

This slope's discontinuity indicates how many locations constitute the core area. Based on the curve shown in figure 2.8, it seems that the mean core area for lorises should consist of 90% of fixes.

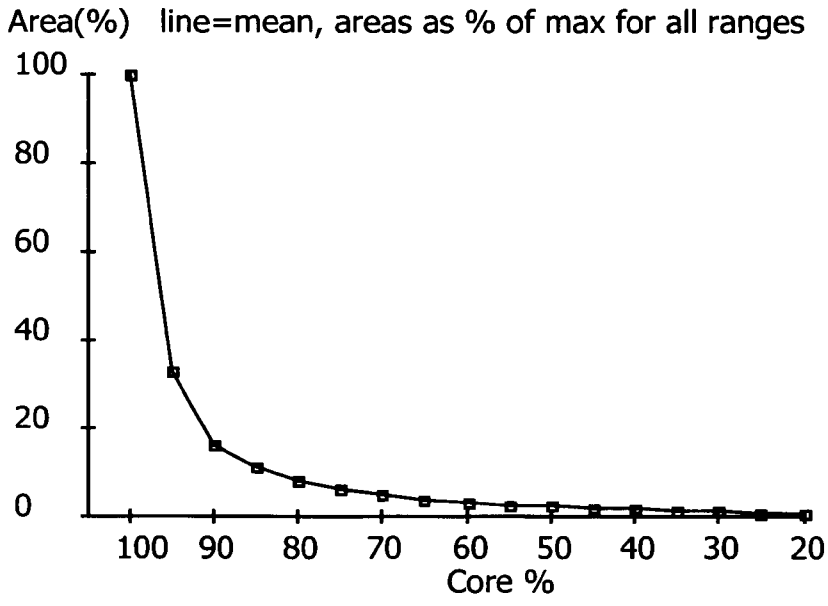


Figure 2.8. Utilisation distribution curve used to assess by eye the percentage of locations needed to estimate core area. The point at which the slope of the plot, which is initially steep as outlying locations are far from the range centre, becomes shallower, represents the percentage of location fixes below which the core locations remain (i.e. <90%).

2. By testing for a difference in proportion of total home range size between 'core areas' (estimated using the KDE method) obtained at 5% intervals.

For each individual I calculated the difference in home range size obtained using different percentage of fixes (at five percent intervals) between two consecutive values (e.g. at 20% and 25% of fixes). I then divided this value by the total home range size (obtained with 100% of fixes) to obtain a relative value of home range size increase. For example for individual X, the relative increase in HR size in relation to total home range size between values obtained using 20% and 25% of fixes resulted in a 3% increase ([0.21 ha - 0.12ha]/3.05ha = 0.029). For that same individual the relative increase in HR size between 25% and 30% remained at 3% ([0.3 – 0.21]/3.05 = 0.030) and between 35% and 40%, resulted in a 3.3% increase ([0.4 – 0.3]/3.05 = 0.033) and so on until 85% of fixes. From that point on the relative difference in home

range size increases sharply (The relative increase in HR size between 85 and 90% = (2.06 – 1.85)/3.05 = 6.9% and between 90 and 95% = (2.38 – 2.06)/3.05 = 10%).

Results from a Friedman test reveal a significant increase in relative home range size as percentage of fixes increased by 5% (Chi-Square = 101.609; d.f. = 15; $p < 0.01$). Since no post-hoc tests are available for this non-parametric test, I conducted a Wilcoxon matched-pairs signed rank test to identify where the difference lied. Thus, I tested for a significant difference in percentage home range size increase as the number of fixes increased at 5% intervals, resulting in a total of 15 pairs (20-25%; 25-30%; ....90-95%). There was a significant increase in the proportion of total area between the 85-90% core areas and the 90-95% core areas (85% and 90%: $Z = -2.38$; $p = 0.016$; 90% and 95%: $Z = -2.521$, $p = 0.008$). Medians of other core areas (20-85%) did not differ. Figure 2.9 illustrates this by showing the steady increase in percentage difference in home range size until 85% of fixes are used, at which point, the difference in home range size sharply increases, suggesting that from that point on, fixes are much further away from the center of activity, resulting in a sudden increase in home range size.

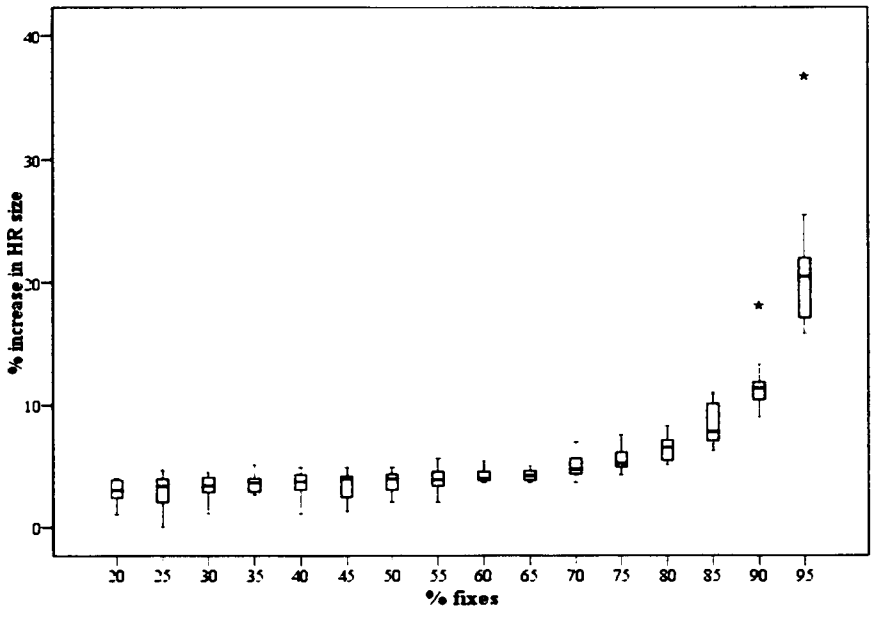


Figure 2.9. Utilisation distribution curve of median percentage increase in home range size as the number of fixes used to calculate home range (using KDE) increases, for 13 radio-collared individuals.

To analyse changes in home range size between months, I used the MCP (100%) method rather than the KDE method, as the former better illustrated occasional outside forays, which animals may have made due to either changes in food quantity (as a result of seasonal changes) or potential mating seasons.

Autocorrelation: The belief that radio-tracking location points must not be autocorrelated, but instead should be statistically independent from each other, has been the topic of debate for at least two decades (Swihart and Slade, 1985a, b; Thomas and Taylor, 1990). Some believe that autocorrelation of locations causes negatively biased estimates of home range size (Swihart and Slade, 1985a) and thus, location fixes should be independent of each other. This is achieved by using location points separated by a certain time interval (Time To Independence, TTI), so that successive locations cease to be significantly correlated (Swihart and Slade, 1985a). However, it has been counter-argued that by definition, the concept of a home range

(as defined by Burt, 1943) involves autocorrelated movements (Otis and White, 1999) as animal movement patterns are not random or temporally independent by nature, and therefore, analysing a statistically independent dataset may not provide a realistic description of what is essentially a non-independent phenomenon (Lair, 1987). Many thus argue that subsampling of data to achieve a TTI between points, may not only fail to reduce autocorrelation of location points, but causes redundancy in the data and significant underestimation of home range size and rates of movements (Rooney *et al.* 1998; De Solla *et al.*, 1999; Otis and White, 1999; Swihart and Slade, 1997; Reynolds and Laundre, 1990). Thus, I chose to include all location points available in my analyses, which were all taken at the shortest time interval possible (five minutes), so that the best possible estimation of home range size and use could be obtained and comparability between individuals made possible (Rooney *et al.* 1998; Otis and White, 1999).

As location fixes were taken every five minutes, I was able to calculate the distance travelled each night for each animal, by adding up distances computed by Ranges 7 from one location fix to another. Only nights that included six hours or more of tracking were used to calculate an average distance travelled per hour. To calculate home range defendability I required the following measurements: diameter of home range (diameter of a circle with an area equal that of the home range) (d'); Mean nightly path length (d); Circumference of home range (C). I used three indices of defendability: the index of defendability (D) (Mitani and Rodman, 1979) calculated using the formula $D = d/d'$; The range traversing index (RTI) (Martin, 1981) calculated using the formula $RTI = d/C$; The fractional monitoring index (M) (Lowen and Dunbar, 1994) calculated using the formula $M = N \times sv/d^2$, where N is the number of independently moving lorises, s is the mean detection distance (set at

20m), v is the path length and d is the diameter of a circle with an area that is equal to the home range. The number of independently moving animals is based on the number of animals that shared part of the focal animal's home range. Out of those, only the animals whose movements were independent to those of the focal animal were counted. The independence of movements was evaluated using Jacob's index of cohesiveness (see section 2.6.4, page 53, for a description of how Jacob's Index was used to measure dynamic interactions). The results of the analysis of cohesiveness indicated which dyads showed independence of movements as opposed to animals that were attracted to or avoided each other. For example, the home range of male MH overlapped that of five other individuals. However, the movements of MH were associated with only two of those based on the values obtained from the analysis of dynamic interactions (Jacob's Index values were > 0). Thus, in the case of MH, the number of independently moving animals, N, was three.

Statistical analysis: Data on home range sizes and percentage home range overlap were normally distributed. Thus, I used the paired t-test to compare home range sizes estimated using the MCP and KDE methods. I used the student t-test to test for inter-sexual differences in home range and core area size; differences in percentage overlap (difference between inter-sexual overlap and intra-sexual overlap; differences between female-female overlap and male-male overlap); differences in number of home ranges overlapped (inter-sexual vs intra-sexual). To give the reader an indication of the variability of original data points I provide mean values $\pm$ SD (as a descriptive statistic). When inferential statistics are used, graphs presenting means $\pm$ 2SEs (or t x SE when sample size is small) are added to support results of statistical tests. Tests are two-tailed and significance levels set at $p < 0.05$. P-values between 0.05 and 0.06 are interpreted as tendency towards significance.

2.6.4. Social behaviour data collection and analysis

Data on social behaviour were collected on radio-collared animals and non-collared conspecifics. Radio-collared animals were identified by their radio-frequency so when more than one radio-collared animal were within five metres of each other, identifying each animal using the radio-frequency signal alone was almost impossible, unless signal fluctuating pattern could be related to movement pattern of the animal observed at the time. In cases where visibility was excellent, we could recognize the animal from either its sex, general appearance or in few cases, characteristic features (for example, one of our females FI, had an atrophied left ear, making it very easy to recognize and others had a distinctive median facial stripe (See Appendix 5 for photographs). If in doubt, we recorded the loris as 'unidentified'.

We collected data on social behaviour using instantaneous point sampling at five minute intervals and in the case of vocalisations, using all occurrences sampling (Altmann, 1974). We recorded presence of another animal in three ways: by tuning into frequencies of other radio-collared animals every 15 minutes (and every five minutes once another animal was recorded as present), by regularly scanning the surrounding area, and by locating vocalizations.

Nocturnal primates use senses in addition to vision (olfactory, auditory) to communicate amongst each other (Charles-Dominique, 1977; Bearder *et al.* 2007) and thus, the distance at which animals are said to be in contact may be more than vision alone allows. Studies on nocturnal mammals have used inter-individuals distances (IID) ranging from 10 to 100 metres as cut-off points from which animals would presumably no longer be able to have contact (Nekaris, 2006; Pimley *et al.*, 2005; Schulke and Kappeler, 2003; Gursky, 2000, 2002). Most studies of sociality in

lorisids, in dense rainforest environments, have used a 20 metre cut off point as the maximum distance at which animals were said to be social (based on vision), whilst a study on slow lorises (Wiens, 2002) used a maximum IID of 50 metres as a cut off point on the basis that animals were able to sense each other at that distance, as has been reported for pottos (Charles-Dominique, 1977). However, studies on slender lorises have used a 30 metre cut off point (Nekaris, 2000). Thus, in this study, a focal animal was said to be in social 'contact' if the estimated distance to a conspecific was equal to or less than 30 metres. I also report results on percentage of social interactions at distances within 20 metres and within 10 metres to allow comparison with studies on other nocturnal prosimians that have used these distances. We recorded the nature of the social behaviour based on the methodology used by Clark (1985), Nekaris, (2000) and Pimley *et al.*, (2005) (Table 2.5). Social behaviours were classed as neutral (form of affiliative behaviour but without interactions. Mutual proximity – animals are within 30 metres of each other but their movements are not coordinated), positive (affiliaitve behaviour with interactions that are either direct: allogrooming, playing, mating; or indirect: animals are between five and 30 metres of each other but their movements are coordinated, i.e. one animal moving towards another or staying with another) or negative (agonistic interactions that are either direct: fights; or indirect: animals are between five and 30 metres of each other and actively avoid each other, i.e. one animal moves away from another or chases it off, resulting in animals moving further away from each other as a result). Animals were said to exhibit neutral social behaviour if they were between five and 30 metres of each other and they moved independently of each other.

These forms of social behaviour were still included within the category 'social' following the methodology by Nekaris (2000, 2006) (for slender lorises), Wiens

(2002) (for slow lorises) and Pimley *et al.* (2005) to allow comparison between studies. Additionally, since assessing the nature of the interaction in nocturnal (and often cryptic) animals can be challenging at best of times, I felt it was prudent to include all instances where animals were within a distance at which some form of social behaviour was possible (even if it do not appear as being positive or negative to the observer), as potential social 'interactions' (see Bearder *et al.* 2006). It is also worth bearing in mind that the animals may scent-mark when seeing a conspecific at that distance, which to the observer may not be obvious and the animals may appear to move independently of the other when in fact, some form of cryptic communication may have taken place. Thus, sociality in this study is reported as percentage of times animals are within 30 metres of each other, regardless of the type of social behaviour apparent to the observer.

Table 2.5. Different categories of social interactions recorded based on two main criteria: inter-individual distance (IID) and behaviour.

Social Interactions	**Neutral**	**Positive**	**Negative**
Direct	N/A	IID: < 5 m apart Behaviour: affiliative interactions (e.g. playing, allogrooming)	IID: < 5 m apart Behaviour: agonistic interactions (e.g. fighting)
Indirect	5 m < IID < 30 m Behaviour: movements independent of each other.	5 m < IID < 30 m Behaviour: moving towards other individual or staying between 5 m and 10 m of other individual.	5 m < IID < 30 m Behaviour: chasing off, running away from, and avoiding other individual.

At distances between five and 30 metres, the distinction between independent movements and dependent movements (and thus between neutral and non-neutral social behaviours) was at times challenging due to the difficulty in interpreting the behaviour of small, cryptic and little-studied animals. I thus present here a clarification of how this distinction was made whilst following a focal animal and collecting data at five minute intervals, by presenting scenarios that arose during the study.

1. If during a focal follow, the focal animal moved away from the other individual (present between five and 30 metres away) and the other individual moved accordingly (or vice versa) so as to remain within the same distance (or closer) to the focal animal, then this would be recorded as movements being coordinated (positive indirect interaction).
2. In a situation where two animals were within 30 metres of each other and the focal animal was in one area not moving (foraging or grooming for example), the other individual was in another area (within 30 metres), also not moving, and they both remained so for any given period of time, the distinction between whether the animals were staying with each other or whether this should be recorded as 'mutual proximity' (animals remained within 30 metres of each other for reasons other than wanting to stay near each other), could only be made once one of the animals moved. Thus:
    i. If the movements proved to be coordinated (either one animal moved closer to another or one animal moved away and the other followed), then the previously observed behaviour would be recorded as 'staying with' rather than 'mutual proximity'.

ii. If on the other hand, one animal moved away and the other did not follow, the previously observed behaviour would be recorded as 'mutual proximity' and carry on being recorded as such until the two animals were more than 30 metres apart.

iii. If the two animals were moving together then stopped and remained together (at distances between five and 30 metres), but one eventually moved away without the other following, then the interactions between the animals when they were not moving would be recorded as 'staying with' and then switched to 'mutual proximity' once one animal moved off (and the other didn't follow).

iv. Finally, if after being near each other for a certain period of time, one of the two animals suddenly chased away the other animal, then the previous time animals spent within 30 metres of each other would be recorded as 'mutual proximity'.

In the context of vocalisations, it was difficult to identify with total certainty the category of social interaction as described in table 2.5. Thus, whenever calls were heard, we simply recorded the inter-individual distance (if more than one animal was present). This was done by a combination of methods. 1) Researchers would scan the area to spot the caller (if the caller was not the animal being tracked) and once spotted one researcher would walk to that location and roughly measure the distance; 2) If the second animal (other than the focal tracked animal) also was radio-collared, the researcher would make a judgement of the distance of the second animal using signal amplitude combined with strength of call; 3) If the second animal could not be spotted or wasn't a radio-tracked individual, two researchers (the two researchers furthest

away from each other out of the team of three) would triangulate the position of the call by taking a bearing of the origin of the call with a compass. Upon return to the field site, the bearing taken by each researcher would be plotted on a map to locate approximate position of the caller and distance.

We were able to work out the maximum distance at which calls could not be heard whilst two teams of researchers were surveying the forest, on several occasions. As one team of researchers separated by a distance of approximately 50 metres from another team, reported hearing a series of calls at very short distance (less than five metres and animal was spotted), the other researchers did not hear the call. This occurred on nights without strong winds or rain and on three separate occasions. Where researchers were separated by approximately 40 metres (on eight separate occasions), both teams heard the calls. However, one team would hear the call very closely whilst the other team struggled to hear and identify the type of call. At a distance of 30 metres or less (> 10 separate occasions), both teams would report the call with certainty and the type of call could be identified correctly by all researchers. Thus, if a call was heard with ease, the animals were judged to be less than 30 metres away from the researchers. If the call was heard but was faint (on a windless and rainless night), the caller was judged to be more than 30 metres away from the researcher. This provided a basis for judging inter-individual distance once distance from the researcher to the animals was worked out using the combination of methods described above.

Sociality was measured in three ways:

1. Using behavioural data I quantified sociality by calculating the percentage of total observed five minute sample points in which each individual was recorded as

being social, and further elucidated this by calculating the percentage of social activities as neutral, positive or negative, and direct or indirect, and recorded the inter-individual distance. In addition, I assessed percentage sociality throughout the night (for each thirteen hourly interval) and percentage sociality in relation to different inter-individual distances.

2. Using behavioural data I measured the degree of contact between individuals (Bearder and Martin, 1980; Pimley *et al.* 2005) using Cole's index (CI) of association (1949). This index was calculated using the following equation: a = 2N/(n1+n2) where N is the number of times animals were seen together and n1 and n2 are the number of times lorises 1 and 2 were observed during the study (Bearder and Martin, 1980). The strength of the relationship between animals that were observed together at some point during the study will be represented by a modified sociogram.

3. Using ranging data (including sleeping site locations) I measured dynamic interactions between individuals. Dynamic interaction is a measure of the attraction, repulsion or indifference between neighbouring individuals. I used temporally coinciding locations to compute the distance between actual locations of an individual and randomly selected potential locations of its neighbour. Because there was some overlap in the neighbourhood of nine simultaneously tracked individuals, I conducted a dynamic interaction analysis to determine if pairs of slender lorises were actively avoiding each other or not, or indifferent.

   I conducted the dynamic interaction analysis using Ranges 7, based on Jacob's Index (Jacob, 1974) (Kenward and Hodder, 1996; Pimley, *et al.*, 2005). The Ranges 7 dynamic interaction analysis gives a single "cohesion" index (Jacob,

1974), for the tendency of pairs of animals to be close together at the same time (The way that Ranges 7 calculates Jacob's Index is described in Kenward *et al.* (1993)). Jacob's Index (Jacob, 1974), which is a modification of Ivlev's Electivity Index (Ivlev, 1961), compares the relative availability of an item in the environment (p) with the relative use of that item (r) and is calculated with the formula:

D = (r –p)/(r+p-2rp). D varies from -1 (negative selection), to +1 (positive selection).

In the case of dynamic interactions, Ranges 7 calculates, for two individuals, the mean observed distance between 'same-time' location pairs (obs) and then the mean of the distance between all possible combinations of location pairs (rnd). A Jacob's Index value is then calculated using the formula:

D = (rndP – obsP)/rndP+obsP – 2* rndP* obsP)

Where rndP = rnd/(rnd+obs) and obsP = obs/(rnd+obs).

Jacob's values approaching 1.0 indicate that simultaneous locations of a pair are closer to each other than the distance between their home range centre given equal likelihood that they could be anywhere on their home range at that time. Values approaching -1.0 indicate that individuals are farther away from each other than by chance alone.

Statistical analysis: I tested for inter-sexual differences in percentage sociality and in values of CI of association using the MWU test and differences in sociality between all hours of the night using the Friedman test for repeated measures. I also tested whether different behaviours occurred at different frequencies depending on inter-

individual distances using the Friedman test for repeated measures (only animals tested across the different conditions were used in the analysis). Median and ranges of values are presented in the form of a boxplot or in the text. Tests are two-tailed and significance levels set at $p < 0.05$. P-values between 0.05 and 0.06 were interpreted as tendency towards significance.

2.6.5. Vocalisation data collection and recordings

With vocalisation data I aimed to assess the three following aspects of loris vocal behaviour:

1. Vocal repertoire of lorises in MPFR, by describing all call types heard in MPFR.
2. Calling frequency of different call types and inter- and intra-sexual differences.
3. Context of different call types.

Data were collected from 2004 to 2006 and calls recorded opportunistically during the radio tracking period (2005 to 2006) on a Marantz PMD tape recorder (40-14,000 Hz) with an AudioTechnica (20-20,000 Hz) unidirectional microphone. Upon hearing a call the following information was collected: sex and identity of caller, identity of animal being tracked, time of night, call type and context of call. The call type was identified based on calls that had been previously described from the wild and captivity (Schulze and Meier, 1995; Nekaris, 2000; Coultas, 2002). They are each distinctive and easily identifiable without needing spectrographic analysis. One possible exception is the whistle, one of the calls uttered by the loris, which is a pulsed call made up of tones (units/syllables), and varies with regards to the number of tones (Schulze and Meier, 1995; Nekaris, 2000; Coultas, 2002) and thus, the

whistle was further qualitatively described based of the number and length of tones that made up the call. Some of the calls that were audio-recorded and displayed spectrographically showed the presence of a tone that was not heard by the researcher at the time of the call, resulting in the whistle being given the wrong number of tones (so a four-tone call may have been recorded by mistake as a three-tone call if the last tone was too short and soft to be heard). Thus, spectrographic displays were used to compare the reliability of our whistle description in the field (with regards to the number of tones that make up the whistle call, as recorded in the field by the researcher) (see Statistical Analysis below for details).

Whenever possible, calls would be allocated to one of three broad context categories: exchanges between conspecifics, calls uttered by only one animal, and calls uttered in the presence of predators. The first context was further subdivided into the following categories: exchanges between unidentified animals (context of call unknown), between a male and a female not part of a sleeping group (those could be agonistic and territorial, or in the context of a female in oestrous), between two females or two males not part of a sleeping group (territorial), between a male and a female pair of the same group (affiliative) and between a mother and its infant. Thus, the context was not determined by what the animal was doing during, before or after the call, but simply by the identity of conspecifics present at the time the call was heard (give or take five minutes). This was due to the fact that the animal calling was rarely observed at the time of the call and its behaviour or that of nearby conspecifics could not be determined. The best that could be done in this situation was to simply record who was present at the time of the call, which gave a broad indication of context (as described above).

A total of 180 whistles were digitised using *Audacity* software (Soundforge, 2006) with a sampling rate of 44,000 Hz. Spectrographic displays of whistles were obtained using *Sound Ruler* (Gridi-Papp, 2004) and used to further subdivide different categories of whistles based on visual features of spectrograms (Davies, 2007). Some of the calls that were recorded and displayed spectrographically showed the presence of a tone that was not heard at the time of the call, resulting in the whistle being given the wrong number of tones (so a four-tone call may have been recorded by mistake as a three-tone call if the last tone was too short and soft to be heard). Thus, spectrographic displays also were used to compare the reliability of our whistle description in the field (with regards to the number of tones that make up the whistle call, as recorded in the field by the researcher) using a Wilcoxon matched-pairs signed ranks test (see Statistical Analysis below for details). The majority of recordings were made during focal follows. Individuals were followed from approximately 18.00 to 06.00, with an average of 6.5 hours $\pm$ 2.7 per night. Behavioural data relating to context were collected on 14 adults (seven male and seven female) and one infant.

Statistical analysis: I compared average calling rate inter-sexually using the MWU test. The Wilcoxon matched-pairs signed ranks test was used to see if there was any significant difference between the numbers of tones assigned to the whistles recorded in the field against the 'actual' number of tones that made up those same whistles, as identified by spectrographic analysis. Due to the difficulty in identifying the caller, I based tests of inter-sexual difference on two data sets: calls that were assigned to an animal of known sex (caller identified) and calls that could not be assigned to an animal of known sex but uttered in the vicinity of an animal whose sex was known (caller unidentified) (since there was the possibility that some of those calls were uttered by the animal of known sex or that the sex of the animal in question influenced the rate of calls

uttered. Median and ranges of values are presented in the form of a boxplot or in the text. All tests are two-tailed and levels of significance set at $p < 0.05$. P-values between 0.05 and 0.06 were interpreted as near significance.

2.6.6. Habitat and microhabitat use data collection and analysis

Using data collected during vegetation surveys and behavioural data collected on radio-collared individuals I aimed to:

1. Assess whether loris density varied within MPFR
2. Evaluate whether lorises used all habitat types within and around the forest, including anthropogenically disturbed habitats, and whether lorises show preference for certain habitat types.
3. Describe microhabitat use and test for inter-sexual differences.

Data were collected on radio-collared lorises between August 2005 and July 2006. Of the 21 collared animals, only 17 (nine males and eight females) had enough data points for statistical analysis. During focal follows the habitat type used was recorded every five minutes and placed into one of the following categories: forest plantations (pine plantations and rubber plantations), agricultural land (paddy fields, banana plantations, cinnamon plantations), home gardens (along the forest periphery), regenerating land (forest plantations and agricultural land left to regenerate), forest. Within the category forest I distinguished between using the edge of the forest and the forest interior.

Edge habitat, or that habitat characteristic of the boundary between a natural environment (e.g. forests) and an unnatural environment (e.g. developed land), results in an edge effect occurring on the natural system. This effect is especially pronounced in small habitat fragments, such as MPFR, where it may extend throughout the patch. Thus, the entire of MPFR forest may be seen as being affected by edge effects and as a result, the distinction between edge habitat and 'natural habitat' becomes difficult to make. This is particularly so since MPFR is highly disturbed and fragmented. However, within this edge habitat, there is an area along the perimeter of the forest patch (where forest meets a paddy field, a plantation, a home garden or a developed area) where the microhabitat shows a marked (visual) difference in vegetation structure and composition from the rest of the forest. Lorises being small mammals I was interested in seeing whether or not these areas along the forest patch perimeter, which were generally characterised by a dominance of shrubs and alien species (e.g. *lantana* sp.), or open area with grasses and no trees, would be used preferentially by lorises in comparison to the rest of the forest where microhabitat characteristics differed.

At a distance of up to five metres from the 'clear-cut' patch perimeter, vegetation structure was markedly different from that of the rest of the forest. Vegetation structure stabilised at a distance of 10 m and differences with 'interior' forest were no longer noticeable past that distance. Other studies have used a similar strip width of 10 m to describe edge microhabitat regardless of forest patch size (from five to 150 ha) or forest type (rainforest or temperate forest), based solely on a detected change in vegetation structure and/or composition (e.g. weed invasion, die-off, dry areas, alien species, shrub richness) from the rest of the forest (e.g. Ranney *et al.*, 1981; Chen *et al.* 1992; Anderson *et al.* 2003). However, to make the distinction between what I defined as 'edge' in the initial thesis with the commonly used term 'edge habitat', I will refer to that area along

the perimeter of the forest patch where forest meets unnatural habitat and where microhabitat features are markedly different for a distance of up to 10 m, as 'patch perimeter habitat'. Preference of habitat type was calculated by quantifying availability within each animal's home range and frequency of use of each habitat type. I calculated the amount of interior forest, patch perimeter habitat and regenerating habitat within each loris home range. I did so by overlaying a grid of 10 m x 10 m (calculated based on the scale of the home ranges) over the home range and habitat map each home range and habitat map and counting the number of 10 m x 10 m squares within each habitat type.

Microhabitat characteristics described in Table 2.6 were recorded every five minutes during focal follows. Height could not be estimated to an exact measure and was thus given a value within a range. The observers and I practiced estimating height range by using a tall measuring pole. Substrate size was estimated by judging the size of the substrate relative to the animal following the method by Nekaris (2000). Connectivity within a five meter radius of the animal's location was assessed by visually judging whether substrates were available on all four sides of the animal's current location so that it would be able to move onto another substrate at any direction (an imaginative five meter radius was split into four quarters. If the presence of substrates, at any height, allowed the animal to move to another location, outside the five meter radius, within each of the quarters, 76 – 100% connectivity would be recorded. The presence of connecting substrates in only one quarter of the radius would result in 0-25% connectivity). In addition, we recorded whether lianas were rare or absent (one liana or less), occasional (two to three lianas), frequent (four to five lianas) or abundant (more than five lianas). Due to the difficulty in identifying all plant species at night, only the eight most dominant species identified during vegetation surveys, were recorded. Inter-observer reliability was frequently tested.

Table 2.6. Microhabitat variables recorded upon sighting an animal.

Microhabitat characteristics	Description
Animal height	< 2 m; 3-5 m; 6-8 m; 9-11 m; > 12 m
Substrate type	Branches, terminal branches, lianas, vines, tangles, trunk, ground.
Substrate orientation	Horizontal (0 to 15°)
	Oblique (15 to 75°)
	Vertical (75 to 90°)
Substrate size	< 5 cm; 6-10 cm; 11-15 cm; > 15 cm
Connectivity within a 5 m radius	0-25%; 26-50%; 51-75%; 76-100%
Abundance of lianas	Rare/absent, occasional, frequent, abundant.
Plant species	Based on the eight most dominant plant species at MPFR

I also assessed percentage connectivity available within the study site by randomly selecting 130 trees and measuring connectivity and abundance of lianas within a five meter radius of each tree, using the method described above.

Statistical analysis: To account for lack of independence of five minute observations, percentages for each variable and each animal, were calculated (as percentage of total observations for each individual, making each individual loris the sampling unit). Inter-sexual differences were tested using the MWU test. I used the Wilcoxon matched pairs test to examine the difference between percentage availability of different habitat types against percentage us by lorises of each habitat type. Median and ranges of values are presented in the form of a boxplot or in the text. Tests are two-tailed and significance levels set at $p < 0.05$. P-values between 0.05 and 0.06 were interpreted as tendency towards significance.

2.6.7. Abiotic influences

Using data on activity, behaviour and home range size I aimed to assess the following:

1. The effect of monthly variations in rainfall, temperature and moonlight on activity, home range size and nightly path length.
2. The effect of moon phase (bright or dark nights) on activity budget.
3. The effect of moonlight on calling rate.

Data on daily temperature and monthly rainfall (daily rainfall figures were not available) were obtained from the records of the Andapana Estate, of Maturata Plantations Ltd, situated 2.3 kilometres from MPFR. I used temperatures recorded at 04.00 and calculated a monthly average by using only temperatures recorded on the nights that animals were tracked. Moonlight was expressed as the night illumination index (NII) obtained using the program NewMoon v.1 (Thomas, 2003). I calculated an average monthly NII by using only NII figures for the nights that animals were tracked in each month. Activity was measured as an average percentage activity score per month for each loris. Home range and nightly path length also were measured as an average per month for each loris.

Statistical analysis: To assess the effect of rainfall, temperature and moonlight on lorises, I first tested for inter-sexual differences in activity using the MWU test. No difference in activity frequency was found between sexes. Therefore, all individuals were pooled to provide an average percentage activity score per month for all lorises. The data set was then tested for multicollinearity, normality, linearity and homoscedasticity. All assumptions were met, which allowed me to conduct multiple

regression analysis to test which of the three abiotic factors best predicted variance in activity scores. I tested the effect of rainfall and temperature on home range size and nightly path length using the non-parametric Spearman's rank order correlation as the assumptions for linear regression analysis were not met for this data set. I tested for differences in percentage activity recorded during dark nights (< 50% illumination) and during bright nights (> 50% illumination) using the Wilcoxon matched pairs test. I tested the frequency with which different behavioural categories were recorded during dark nights and during bright nights using the MWU test. The Bonferroni correction was applied when testing data sets multiple times. I tested the relationship between NII and calling frequency using the parametric Pearson correlation.

2.6.8. Ethical Note

I conducted this study with the permission of Sri Lanka's Department of Wildlife Conservation, Forestry Department, Ministry of the Environment, Ministry of Defence and the Telecommunications Regulatory Commission of Sri Lanka. The study was granted permission based on the fact that a local Sri Lankan professor (Prof. A. Gunawardena from the University of Ruhuna) agreed to act as Principal Investigator of this research. The approval of the local senior Buddhist monk and the local village chief also were obtained prior to the start of the study.

All procedures involving the collection of data on lorises followed the guidelines for animal care and use of animals (Animal Care and Use Committee, 1998). Lorises in this study were not trapped or kept in enclosures and were released as quickly as possible back to the same location within which they were caught (see section 2.5.2.). Only lorises weighing over 110g were collared to ensure that the collar would not be more than five percent of its body weight (see Gursky, 1998).

CHAPTER 3 RESULTS

This chapter is divided into three broad topics: the first one is descriptive in nature and comprises: a description of the study site and the study population and a section describing general behavioural traits of lorises at MPFR, including a detailed behavioural ethogram, general activity budget and daily activity rhythms. The second topic covers the results on the social organisation of lorises at MPFR, which I elucidate by describing and analysing ranging patterns, followed by a description and analysis of their social interactions. The final topic relates to the ecological plasticity of lorises at MPFR and comprises the following elements: habitat and microhabitat use, and influence of abiotic factors on behaviour.

3.1. THE STUDY SITE

3.1.1. Total area reduction of MPFR

A map of MPFR dating back to 1968 was compared with one prepared in 1985 (revised in 1999) and a satellite map obtained from Google Earth in 2006, to evaluate whether MPFR had changed in size and/or shape. Figure 3.1 illustrates the outline of each map, thus showing the change in forest extent since 1968.

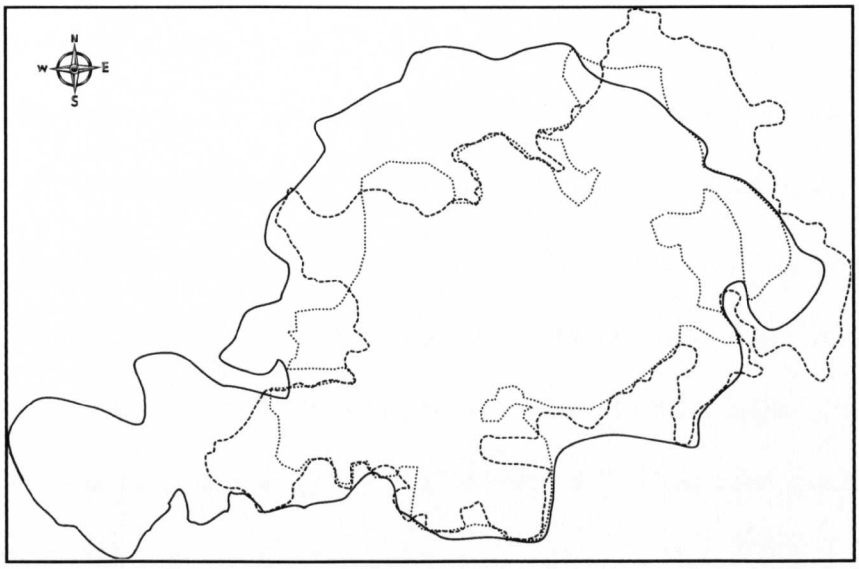


Figure 3.1. Outline of MPFR in 1968 (in bold), in 1999 (in a dashed line) and in 2006 (in a dotted line). This map is at a scale of 1:50,000.

Despite some of parts of the forest increasing in extent (North-eastern side), overall, the forest decreased in area by 30.6% from 1968 to 1999, and by 21.7% since 1999 to 2006. The area that increased from 1968 to 1985 initially consisted of plantations (cinnamon, banana, cardamom, tea, etc) but were subsequently abandoned and left to regenerate into scrubland. This scrubland was then from 1985 to the present day, cleared for human settlement.

3.1.2. Forest structure and floristic composition

A total of 67 species were found at MPFR, 58 of which were identified and belonged to 34 families (Appendix 6). The most represented family was Euphorbiaceae. The majority of species were endemic (52 %; n = 30) and native (41 %; n = 24), whilst only four species were introduced or exotic. In terms of sites where tree species are typically found, only 12 % are typical of secondary/disturbed sites and 10 % are

typically found in home gardens and forest edge. About 48 % are typically found in wet-evergreen forests (rainforests), 28 % in moist semi-evergreen forests (intermediate forests) and 19 % in monsoonal forests. So although historical records show that MPFR has been heavily exploited, it is nevertheless a floristically interesting forest as it is found in a zone where plant species typical of each of the three climatic zones of Sri Lanka, the Dry Zone, the Intermediate Zone and the Wet Zone, occur together. The majority of species found at MPFR are subcanopy species (34 %), and understorey species (28 %), whilst only 18 % of recorded species are canopy species.

Density of trees with a CBH > 10 cm was 1901 (± 528) trees per hectare, whilst the average basal area of 527 trees surveyed was 556.4 ± 22.1 m^2/ha. Of all species surveyed, *Humboldtia laurifolia* had the highest basal area with 149.9 ± 139.2 m^2/ha. Average tree height at MPFR was 12.3 ± 5.5 m. The ten most dominant tree species across the study area were, in order of decreasing importance: *H. laurifolia*, *Swietenia macrophylla*, *Dipterocarpus zeylanicus*, *Artocarpus nobilis*, *Semecarpus walkeri*, *Mangifera zeylanica*, *Dillenia retusa*, *Actephila excels*, *Horsfieldia iriyaghedhi* and *Bhesa ceylanica* (Appendix 7).The species *H. laurifolia* had the highest density, frequency and basal area overall. The second and third most dominant species, *S. macrophylla* and *D. zeylanicus*, had nearly equal IVI values but the former was as a result of relatively high frequency and the latter as a result of relatively high basal area. Differences in floristic composition and stand characteristics within the study site are presented in relation to slender loris density, in the 'Habitat Use' section of this chapter (section 3.4.1).

3.1.3. Some mammal species present at MPFR and encounter rates

We encountered the following mammal species during diurnal surveys: toque macaque (*Macaca sinica aurifrons*), purple-faced langur (*Trachypithecus vetulus vetulus*), Sri Lankan giant squirrel (*Ratufa macroura*) and squirrel (*Funambulus* spp.). The purple-faced langur was more frequently encountered across MPFR (Mean = 0.23 groups / km) than the toque macaque (Mean = 0.16 groups / km). Table 3.1 provides the encounter rates for each species along each path walked.

Table 3.1. Encounter rate (individuals per kilometre walked) for *Trachypithecus vetulus vetulus* and *Macaca sinica aurifrons* along five paths in MPFR during diurnal surveys (N = 65). VP = Village Path, NST = North to South Trail, SP = Stream Path. See Figure 2.5 for position of each of these paths in MPFR.

Surveyed paths		**VP1**	**VP2**	**VP3**	**NST**	**SP**	**Total for MPFR**
Total path length walked (km)		24.4	23.5	9.6	17.6	36	111.1
T. v. vetulus	Number of groups encountered	6	9	2	0	9	26
	Encounter rate (grps/km)	0.25	0.38	0.21	0	0.25	0.23
M. s. aurifrons	Number of groups encountered	8	6	0	0	4	18
	Encounter rate (grps/km)	0.33	0.26	0	0	0.11	0.16

The toque macaques and the purple-faced leaf monkeys lived sympatrically within MPFR but avoided competition by using different areas at different times. The macaques appeared to move around much larger areas and in larger groups (Mean = 8.7, range = 6 – 12, N = 18), unlike the resident langurs, which appeared to have more stable home ranges and travelled in smaller groups, sometimes consisting of a lone male (Mean = 3.8, range = 1 – 6, N = 26). They were frequently seen in the daytime within slender loris ranges, including areas where lorises were known to sleep. They

occurred in single male groups of up to three or small groups, including males, females and juveniles, of up to six. Lone males also were observed and heard calling at the periphery of the study site. Although observed more frequently within the forest, the langurs were also observed in home gardens surrounding the forest, feeding on fruits of mango trees and jackfruit trees. These trees also were found within the forest; particularly mango trees. They also were observed feeding on the fruits of *Dillenia retusa* and *Artocarpus nobilis*, two dominant endemic species across MPFR (see Table 3.2 for IVI of tree species). The macaques made use of forest plantations and grazing fields to travel from one part of the forest to another, unlike the langurs who used home gardens and forest edge instead.

During nocturnal surveys we recorded the encounter rate for the following species: fishing cat (*Felis viverrina*), rusty-spotted cat (*Felis rubiginosa*), golden palm-civet (*Paradoxurus zeylonensis*), common palm-civet (*Paradoxurus hermaphroditus*), small Indian civet (*Viverricula indica*), Indian brown mongoose (*Herpestes fuscus*), Eurasian otter (*Lutra lutra*), Indian crested porcupine (*Hystrix indica*), white-spotted chevrotain (or mouse deer) (*Moschiola kathygre*) and Eurasian wild boar (*Sus scrofa*) (Table 3.2). Other mammal species observed but not recorded during surveys were: giant squirrel (*Ratoufa macroura*), the common palm squirrel (*Funambulus palmarum*), the five-striped squirrel (*Funambulus penantii*), the greater bandicoot rat (*Bandicoot indica*) and the Ceylon field mouse (*Mus cervicolor fulvidiventris*) (Appendix 8). Although bats were present at MPFR, we did not attempt to identify them.

Table 3.2. Encounter rate (individuals per kilometre walked) for all mammal species (except bats) encountered during nocturnal surveys (N =133). VP = Village Path, NST = North to South Trail, SP = Stream Path. See Figure 2.5 for position of each of these paths in MPFR.

Species	Surveyed Paths					Mean encounter rate across MPFR
	VP1	VP2	VP3	NST	SP	
L. t. tardigradus	2.00	1.06	0.13	0.23	0.09	0.70
M. kathygre	0.98	0.09	0.86	0.14	0.40	0.49
H. indica	0.88	0.08	0.16	0.22	0.03	0.27
S. scrofa	0.04	0.31	0.07	0.06	0	0.10
P. zeylonensis	0.08	0.18	0.15	0.03	0	0.09
P. hermaphroditis	0.05	0.04	0.13	0	0	0.04
V. indica	0.10	0.10	0.02	0.03	0	0.05
F. viverrina	0.03	0	0	0	0	0.006
F. rubiginosa	0.02	0	0	0	0	0.004
H. fuscus	0.02	0	0	0	0	0.004
L. lutra	0	0.01	0	0	0	0.002

The loris was the most frequently encountered mammal in MPFR particularly along path VP1 and VP2. Few lorises were encountered along path VP3, particularly the section of the path running along the paddy field, and along path SP running alongside a pine forest plantation (Figure 2.5). Significantly more lorises were encountered during dark moon phases (N = 119) than bright moon phases (N = 53) (MWU = 903.5, $n_1 = 119$, $n_2 = 53$, $z = -2.914$, $p = 0.004$) (Table 3.3).

Table 3.3. Comparison of average number of lorises sighted during dark nights and bright nights.

Moon Luminosity	Mean encounter rate	SD	Median
Dark nights (N = 55)	2.42	2.45	2.00
Bright nights (N = 47)	1.19	1.51	1.00

The mouse deer was the second most sighted species and was seen foraging alone or in pairs. Mouse deer were extremely shy and if startled, would flee whilst emitting a loud squeaky sound which had the effect of alerting other animals, including the loris. The Sri Lankan mouse deer, has recently been recognised as a distinct species (*Moschiola kathygre*) by Groves and Meijaard (2005), being split from *Moschiola meeminna,* and based on morphologically distinct features. This taxonomic pattern may be found across all mammals of Sri Lanka's biodiversity rich Wet Zone.

The porcupine was the third most frequently encountered mammal in MPFR. It usually foraged and travelled alone but two porcupines were once observed chasing each other through the forest. The males were extremely territorial and aggressive towards my assistants and me whenever we encroached into their territory. We would then be met by a porcupine rattling its quills, stomping its feet and angrily charging at us whilst making a loud call.

The wild boar was the largest mammal found in MPFR and the fourth most frequently encountered mammal at night. Although wild boars travelled in large groups (up to 18) at dawn and dusk, to and from their sleeping sites, they were mostly encountered foraging alone or in pairs (mother and infant).

The civets were relatively frequently sighted. The golden palm-civet and common

palm-civet were always found on branches of relatively tall trees but the golden palm-civet also was observed using the smaller *Humboldtia laurifolia* tree species in area SS2. These carnivores were observed on two occasions attempting to catch lorises and were often encountered within 20 metres of lorises (N = 14). The ring-tailed civet on the other hand was always seen travelling on the ground and never made attempts to catch lorises, and did not elicit any reactions from the latter when within less than five meters away (N = 3).

The fishing-cat and rusty-spotted cat were rarely seen. The former was seen once within 10 metres of a loris mother and her infant being chased by one of the radio-collared males MA and making chitter calls (see Section 3.3.1 for description of call). The fishing-cat was resting on a branch of *H. laurifolia* and neither appeared to pay attention to the other. The rusty-spotted cat also was rarely seen and never in the proximity of a loris.

3.1.4. Climate

Figure 3.2 shows rainfall patterns between January 2004 and August 2006. Rainfall patterns are unpredictable. The year 2004 showed distinct seasonality with the dry season occurring between January and May (precipitation < 100 mm) and the wet season occurring between August and December. Years 2005 and 2006 on the other hand showed very little variation, no distinct seasonality patterns, and generally less rain than 2004 (Figure 3.2). Data for 2006 were available only until August, but average rainfall between January and August 2005 (Mean = 120 mm $\pm$ 82) are similar to those between January and August 2006 ($\bar{x}$ = 175 mm $\pm$ 73). Temperature patterns were more predictable across the 32 months between January 2004 and August 2006.

Temperatures reached their highest between May and December followed by the lowest temperatures between January and March in both 2005 and 2006.

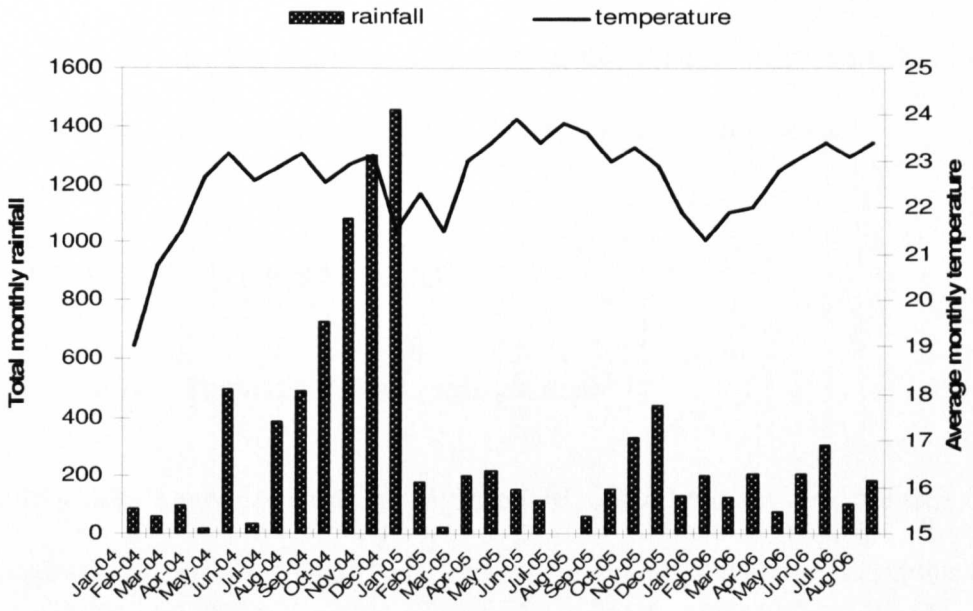


Figure 3.2. Total monthly rainfall and average monthly temperatures from January 2004 to August 2006.

Summary

- The study site within MPFR measured approximately 85 hectares of which 24 consisted of rice paddies and pine forest plantations. Vegetation surveys revealed a total of 67 tree species belonging to 34 families, of which 52 % were endemic and 41 % native to Sri Lanka. Density of trees (with a CBH > 10 cm) was 1901/ha $\pm$ 528, average basal area: 556.4 $\pm$ 22.1 m²/ha and average height of trees with a CBH > 30 cm was 12.3 m $\pm$ 5.5. The most dominant plant species were *Humboldtia laurifolia*, *Swietenia macrophylla* and *Dipterocarpus zeylanicus*.
- Diurnal and nocturnal surveys revealed the presence of 13 species of mammal (excluding bats), including three primate species: *Macaca aurifrons*, *Trachypithecus vetulus* and *Loris tardigradus tardigradus*. The slender loris was

the most encountered animal during nocturnal surveys with a linear abundance of 0.70/km.

- Climate at MPFR was characterised by unpredictable rainfall patterns from one year to the next but a general drop in temperature between the months of January and March and a peak in temperature between June and August.

3.2. THE STUDY POPULATION

3.2.1. Population density and sex ratio

Based on the number of animals caught and associated non-collared animals, I recognised 29 animals, including 21 caught individuals and eight individuals that were not caught but the sex and/or age of which was identified (Table 3.4). Thus, 12 females, 13 males, and two juveniles/infants of undetermined sex were identified. I sighted an additional two non-caught animals (not juveniles, sex unidentified) at dusk and dawn with radio-collared individuals as forming part of their sleeping group, resulting in a total of 29 individuals and a loris density of 0.48/ha (in an area measuring approximately 60 hectares). This population number of 29 individuals probably constitutes a good estimate of the total loris population within the radio-tracking area (at least during the duration of the study period) as no other individual was seen sharing the sleeping sites of known lorises or seen interacting with known lorises. In addition, during the later months of radio-tracking lorises, no 'new' lorises were encountered. Finally, movements in and out of the part of MPFR where the radio-tracking site was situated, would have been difficult for lorises as a result of that part of the forest being almost completely disconnected from other parts of MPFR by

pine forest plantations, paddy fields and a stream (see Figure 2.5). This point is discussed further on in the thesis in section 4.1.1.

Table 3.4. List of all lorises identified within the study site, including radio-collared males and females, non-collared males and females, caught juveniles, and infants carried by identified females (one radio-collared female and one non-collared female).

Loris ID	**Date caught**	**Age**	**Weight (g)**	**Reproductive status of females and parking behaviour of infants**
FE	08.12.2005	Adult	153	Mature, possibly pregnant
FB	09.12.2005	Adult	117	Nulliparous when caught then gave birth.
FR	02.07.2006	Subadult	110	Nulliparous
FF	16.09.2005	Adult	133	Multiparous
FM	06.04.2006	Adult	129	Nulliparous
FI	15.01.2006	Adult	114	Nulliparous
FK	04.03.2006	Adult	149	Possibly pregnant or recently gave birth.
FG	07.02.2006	Subadult	116	Nulliparous
FJ	27.07.2005	Subadult	111	Nulliparous
F 1	N/A	Adult	?	Breastfeeding
F 2	N/A	Adult	?	Breastfeeding
F 3	N/A	Adult	?	Breastfeeding
MA	07.08.2005	Adult	150	
Ma	20.10.2005	Adult	150	
MJ	31.07.2005	Adult	160	
MT	31.10.2005	Adult	144	
MO	26.03.2006	Adult	139	
ML	02.04.2006	Adult	139	
MD	18.08.2005	Adult	171	
MC	11.12.2005	Adult	138	
MH	27.02.2006	Adult	124	
M 1	N/A	Adult	?	
MJ1	11.06.2006	Juvenile (~1 mo)	30	Parked, small home range
MJ2	09.11.2005	Juvenile (~2.5 – 3 mo)	75	Parked, but independent movement
MJ3	07.01.2006	Juvenile (~2-2.5 mo)	71	Parked but independent movement
J4	Month of birth: April 06	Infant	?	Carried by mother FB at all times
J5	Sighted with mother in August 05	Juvenile	?	Not parked but within short distance of mother. Independent movements
UL1	12.05-04.05	Adult?	?	Part of a group (FB and MD)
UL2	04.06-05.06	Adult ?	?	Part of a group(FM and ML)
29 lorises. Male: female ratio: 1: 0.92				

Based on identified individuals at the study site (including infants), the sex ratio at MPFR was 13 males to 12 females (1:0.92). The sex of the additional four lorises (two juveniles and two non-juveniles) could not be determined with complete certainty. Young males could easily be mistaken for females and thus no assumptions were made. Either way, the ratio would not be strongly biased as female or male, and would remain at approximately 1:1.

A total of twelve females were identified. Nine of those were adults and three categorised as subadults. A total of thirteen males were identified including nine males that were radio-collared, one adult male that was sighted on the home range of the youngest juvenile and recognised by the visible scrotal pigmentation, and three juvenile males ranging from two months to approximately four months of age. Two of the infants of the MPFR population were carried by their mothers (FB and F2) and thus judged to be of less than one month of age. The third youngest infant was parked by its mother at the beginning of the night and checked upon regularly throughout the night by its mother. The mother picked it up again before the end of the night and carried it back to the sleeping site. Movements of this infant were limited to an area of approximately 0.12 hectares. The other two juveniles were judged to be around 2-3 months of age.

3.2.2. Morphometric data and sexual dimorphism

A total of 15 morphometric variables were collected on all caught animals except the three juveniles who were only measured for weight (Appendix 2). Non-juvenile females ranged in weight from 110 g to 153 g. Non-juvenile males ranged in weight from 124 g to 171 g and were significantly heavier than females (Males: Mean weight

= 146.11 g ± 13.71; Females: Mean weight = 125.78 g ± 16.28) (Student t-test: t = 2.86; d.f. = 16; p = 0.01) (Figure 3.3).

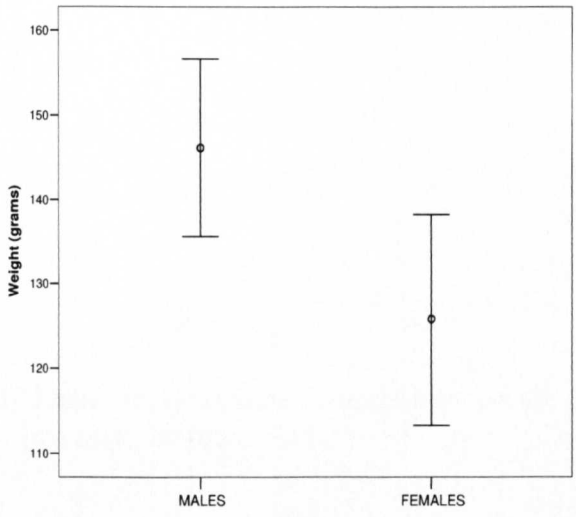


Figure 3.3. Mean weight (g) (± txSE) of caught females (N = 9) and males (N = 9) excluding the three juveniles/infants.

When the subadult female FG is removed from analysis, there is no longer a significant difference in body weight between females (132.8 g ± 15.6) and males (Student t-test: t = 1.80, d.f. = 13, p = 0.09).

Female body length ranged from 136 mm to 235 mm and male body length from 147 mm to 221 mm. There was no significant difference in total body length between females (Mean body length = 195.9 mm ± 3.5) and males (Mean body length = 188.0 mm ± 2.4) (Student t-test: t = -0.56, d.f. = 16, ns) (Figure 3.4).

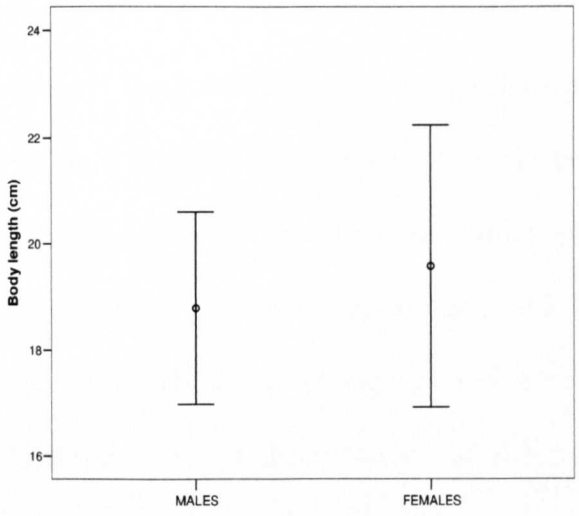


Figure 3.4. Mean body length (cm) (txSE) of caught females (N = 9) and males (N = 9) excluding the three juveniles/infants.

The degree of sexual dimorphism calculated was 116.1 for weight and 95.9 for body length.

3.2.3. Reproductive characteristics

Male lorises at MPFR had a mean testis volume of 2127 $mm^3 \pm 815$, and varied between 1084 mm^3 and 3216 mm^3 (Figure 3.5).

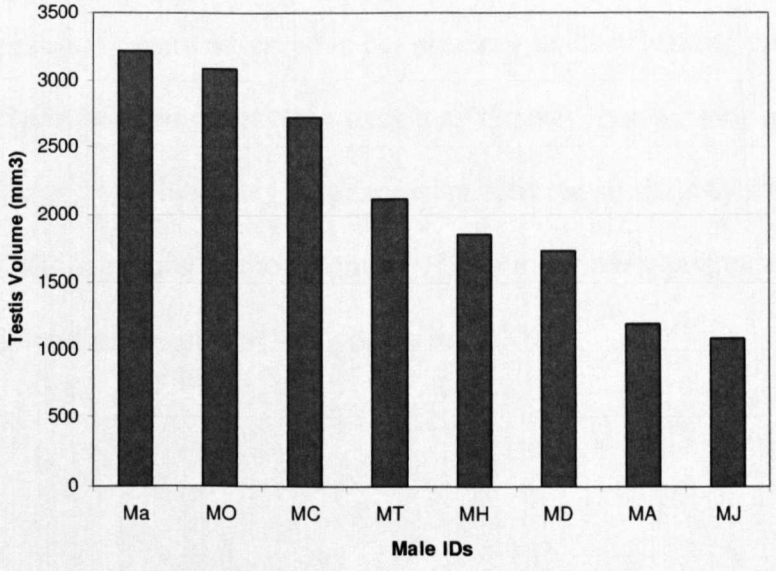


Figure 3.5. Testis volume of eight radio-collared males.

This was compared to testis size of other strepsirrhine species using a logarithmic plot of mean testis volume over body weight for 21 prosimian species (using data from captive animals) (Kappeler, 1997b). Based on the linear regression line between these two variables, the predicted testis volume for prosimians of similar weight was approximately 615 mm^3. The actual average testis size for *L. t. tardigradus* at MPFR was 3.5 times bigger than this predicted value. The actual average testis size for *L. t. tardigradus* at MPFR was 3.5 times bigger than this predicted value, and although large variation was found between males in testis size, even the smallest testes were 1.5 times larger than the predicted value of 615 mm^3.

The reproductive characteristics of females at MPFR included whether the vaginal cleft was visible or not and if visible whether it was reddened or not, thus distinguishing between pre-oestrous or oestrous states. The mammary glands also were inspected to determine whether the female was nulliparous or multiparous or lactating (Table 3.5). Two of the eight females caught had open and reddened vaginal clefts. One was caught in April and the other in May. Three of the females showed signs of having breastfed in the past and one showed possible signs of lactating when caught but no offspring were observed in her presence in the following months. One female would have been pregnant when caught as she was seen carrying an infant five months later. No signs of her being pregnant were detected so she may have been caught right at the beginning of the pregnancy. Even in captivity pregnancy is notoriously difficult to detect (Fitch-Snyder *et al.*, 2001).

Table 3.5. Reproductive characteristics of females caught, including their weight, appearance of the vaginal cleft and inferred reproductive status, and appearance of their mammary glands and inferred signs of nulliparity or multiparity. The date when females were caught is included to identify potential reproductive seasons.

ID	Date caught	Weight (g)	Vaginal cleft and reproductive status	Signs of nulliparity/multiparity
FJ	27.07.05	111	Closed - anoestrous	Unused and non lactating mammary glands – nulliparous.
FF	16.09.05	133	Closed - anoestrous	Used and non lactating mammary glands – multiparous.
FE	08.12.05	153	Closed – anoestrous	Enlarged mammary glands so possibly lactating. Mammary glands used – multiparous.
FB	09.12.05	117	Closed with a dark fur pattern around – anoestrous	Pregnant when caught as gave birth in April. Mammary glands slightly enlarged but unused – nulliparous.
FR	02.07.06	110	Closed - anoestrous	Unused and non lactating mammary glands – nulliparous.
FI	15.01.06	114	Closed - anoestrous	Unused and non lactating mammary glands – nulliparous.
FG	07.02.06	116	Closed - anoestrous	Unused and non lactating mammary glands – nulliparous.
FK	04.03.06	149	Open, reddened and turgid – oestrous	Used and non lactating mammary glands – multiparous
FM	06.04.06	129	Open, reddened and turgid – oestrous	Unused and non lactating mammary glands – nulliparous.

3.3. ETHOGRAM, ACTIVITY BUDGET AND DAILY RHYTHMS

3.3.1. Behavioural ethogram

Although much of the behaviours observed in this study resembled those of captive *Loris lydekkerianus lydekkerianus* described by Schulze and Meier (1995), I nevertheless describe all behaviours exhibited by *L. t. tardigradus* in MPFR as currently no ethogram exists for this species in the wild. I use the same terms used by previous studies on slender loris behaviour (Radakrishna and Singh, 2002; Nekaris, 2000)

POSTURAL AND LOCOMOTORY BEHAVIOURS

Sitting: sitting on a horizontal/oblique substrate with both feet and one or both hands holding onto substrate.

Clinging: holding onto a vertical/oblique substrate with arms and legs wrapped around substrate and abdomen held against substrate.

Quadrupedal standing: standing on a horizontal/oblique substrate, with feet and hands holding on substrate.

Bipedal standing: standing on a horizontal/oblique substrate with feet on substrate, body in an upright position and one or both hands holding onto another substrate, or hands free.

Cantilevering: holding onto a vertical substrate with feet and body in a stretched out horizontal position, perpendicular to the vertical substrate.

Curl: sitting position on horizontal substrate, with head tucked in between knees and hands holding onto substrate in front so that the body forms a ball-shape and face cannot be seen.

Hanging: hanging down from horizontal/oblique substrate, using feet.

Walking: moving quadrupedally on horizontal/oblique substrate.

'Flat walking': moving with body close to substrate.

'Arched walking': moving with limbs stretched out and back slightly curved.

Climbing: vertical ascent or descent.

Bridging: bridging a gap between supports of any orientation.

Walking hanging down: moving quadrupedally under horizontal/oblique substrate.

Travelling: moving without stopping or stopping for less than 10 seconds, generally on a horizontal plane in one direction.

Locomotion: moving whilst stopping regularly along the way to perform other activities.

'To and Fro' locomotion: moving fast in one direction then suddenly turning around and retracing its steps. This can occur several times.

FEEDING BEHAVIOURS

Foraging: the animal was said to be foraging if it was searching for food showing head cocking movements and often focussing on a small area (a branch, a bush, a liana, etc.). Foraging also includes the act of observing and catching prey. Catching prey can occur with one or both hands from a substrate, a leaf or the air.

Feeding: feeding was recorded if the animal was seen putting food in its mouth, by using its hands or by directly catching prey with its mouth, biting food or chewing food.

Drinking: drinking was recorded if the animal was seen licking water from a leaf, water hole or sucking water from a bamboo shoot.

RESTING BEHAVIOURS

Resting: in a sitting position, head not moving and eyes closing down.

Sleeping: animal's eyes closed down for more than 1 minute and usually in curled up position, or semi-curled up with head falling down.

SELF BEHAVIOURS

Self play: hanging upside down, arms stretched out and twisting body side to side.

Autogroom: grooming itself. Grooming was further broken down into the following behaviours:

Scratch: this occurred with the foot using the second digit with the toilet claw. Scratching of ear, throat, and abdomen. After cleaning the ear the foot is always licked.

Lick: gentle back and forth movement of the head involving animal cleaning its body with its tongue.

Toothcomb: vigorous pushing back and forth movement of the head involving animal combing its fur.

Arm over face: gentle brush over the face with the forearm, occurring often more than once in a row and followed by the licking of the arm.

Neck rubbing on substrate: lying on a branch, or flat walking, with head twisting sideways to run neck area onto substrate.

Urine-marking: lowering hindquarters and depositing drops of urine along substrate while locomoting.

SOCIAL BEHAVIOURS

<u>Positive interactions:</u>

Allogroom: grooming another animal involving the toothcomb rather than licking. One or both animals can be grooming at any one time, and take turns. One animal will

usually stretch one arm up, presenting thus the brachial gland area, requesting for that area to be groomed. Animals can be facing each other, or one giving its back to the other, whilst sitting down, or hanging down. Often the animal grooming will hold onto the other one to give it the vigorous toothcomb groom.

Neutral proximity: two animals within 30 metres of each other but not following the other animal and ignoring/tolerating its presence.

Staying with: one animal following the movements of another animal and always remaining within 10 metres.

Play wrestling: two animals hanging upside down facing each other mouth open as if to bite each other but without biting. In some cases this would be terminated by one animal emitting a chitter call. This behaviour can also occur with one animal mounting the other in a copulatory manner.

Mating behaviour: although no act of copulation was observed during this study, behaviours associated with mating events were recognised based on description of mating behaviours made on *L. l. lydekkerianus* and *L. t. tardigradus* in the wild and captivity (Nekaris, 2000; Nekaris, 2003; Radakrishna, 2002; Radakrishna and Singh, 2003; Schulze and Meier, 1995; Izard and Rasmussen, 1985). Prior to copulation a male chases a female staying close behind and uttering appeasing krik calls (see 'vocal repertoire' below for description of call) although those are extremely difficult to hear unless within five metres of the animal. Other males are most probably present in which case one male will chase away the others whilst uttering whistle calls (see 'vocal repertoire' below for description of call). The female may reject either of the males' attempts to mount her by uttering the chitter call (see 'vocal repertoire' below

for description of call). When ready to copulate a female will hang upside down to assume the copulatory position, which resembles that seen in play wrestling.

Negative interactions

Rejections: one animal attempting to play or mate and the other pushing it away with both hands and chittering whilst walking off.

Aggressive staring: one animal stares at another animal generally within five metres – 10 metres, in a way that makes the opponent retreat.

Aggressive display: this involved an animal making jerky movements whilst moving fast and in the process causing substrates to make a rattling noise. Another animal would be within 30 metres.

Avoiding/retreating: animal turning back, away from another loris' home range boundary (other loris may not be present), or away from a loris showing aggressive display, staring or chasing.

Chasing: one animal chases another who retreats. Aggressive chasing may be associated with lunging movements by the chaser as if to attack it. This would occur at distances within 5m.

Fighting: two animals wrestling either standing on a horizontal/oblique substrate or whilst hanging down facing each other. Involves biting, chitter calls, and grabbing of head to bite the nuchal region.

Sexual pursuit: a male chasing a female during pre-oestrous or oestrous keeping very close contact to the ano-genital part of the female's body. The female rapidly moving away or stopping to turn around and reject the male. This is categorised as an

aggressive pursuit as opposed to an affiliative one based purely on the female's reaction. A female that did not reject the attempts by the male or attempt to bite the male would accept the attempts and allow the male to groom her and mate with her. This would then be categorised under affiliative behaviours and mating.

EXPLORATORY BEHAVIOURS

Exploring without moving: animal in a stationary position, scanning surroundings (vigilance) as opposed to the exploratory behaviour associated with searching for food (foraging)

Exploring whilst moving: animal scanning surroundings whilst moving.

BEHAVIOURS ASSOCIATED WITH HUMANS

Freezing: animal in a stationary position, not moving at all, not even the head. This occurred in a situation where animal was not habituated to researchers or when researchers were too close (less than two metres away).

Aggressive: animal biting hand/fingers of person without letting go.

Submissive: once caught the animal generally curled up in a ball and did not move for a few minutes. This varied between animals. Some appeared comfortable being held and climbed all over the researcher, whilst others remained curled up, immobile and tense. In some cases an animal would stretch out an arm, thus showing the armpit. This behaviour may have been similar to the stretching behaviour described by Goonan (1993) as a grooming 'invitation'.

3.3.2. Daily activity rhythms

I calculated monthly average scores (of whether animal was 'active' or 'inactive') for each 13 radio-collared individuals (six females and six non-juvenile males, and one juvenile male) between August 2005 and June 2006. Slender lorises did not move away from their sleeping site until after the end of the nautical twilight (between civil twilight (some sunlight remains) and before astronomical twilight (complete darkness) and where the horizon appears indistinct (the sun is between 6° and 12° below the horizon) - usually around 18.30-18.45). However, activities around the sleeping site, such as grooming, socialising and exploring within the sleeping tree, took place between sunset (between 17.45 and 18.00) and the end of the nautical twilight. Slender lorises reached an activity plateau sometime between 19.00 and 20.00, as they travelled away from their sleeping sites to go foraging. Activity levels remained high (lorises were active about 70 % to 80 % of the time) until 05.00 and 06.00, when activity levels decreased as lorises returned to their sleeping sites and engaged in resting and grooming activities (Figure 3.6).

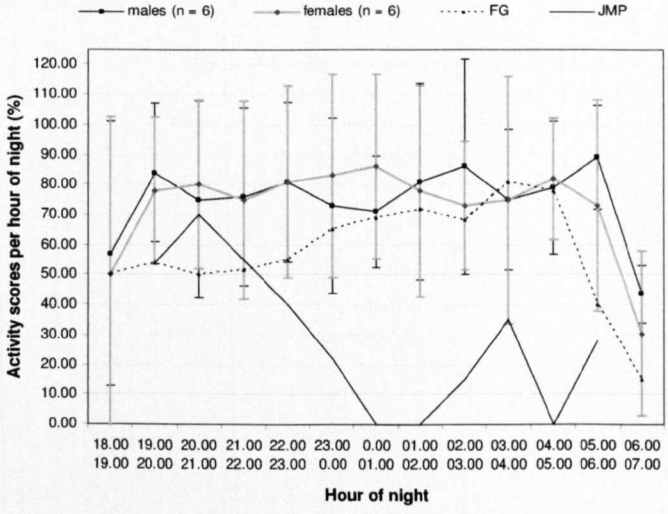


Figure 3.6. Average (± SD) percentage activity scores for six adult males, six adult females, one subadult female (FG), and one juvenile male (JMP), for each hour of the night between 18.00 and 07.00. JMP = Juvenile Male P.

The activity profiles of subadult female FG and juvenile male JMP (approximately one to two months old) were different to that of the other lorises. For female FG, frequency of activity was much lower for most of the night than other females and dropped much earlier in the night. Activity patterns of JMP were characterised by a lower frequency of activity throughout, apart from an initial burst of activity in the early hours of the night (~ 20.00), and a second peak between 03.00 and 04.00. A last peak of activity was noted after 05.00, which coincided with the juvenile joining the mother or being picked up by the mother.

3.3.3. General activity budget

Lorises were recorded as 'active' (Mean = 75.6 % ± 11.2), more frequently than 'inactive'. Active periods were dominated by travelling (26.9 % ± 6.2), followed by foraging (19.5 % ± 9.2), exploring whilst moving (14.9 % ± 5.7) and grooming (11.1 % ± 6.7). Inactive periods consisted of exploring without moving (13.7 % ± 5.4) and resting or sleeping (8.9 % ± 6.2) (Figure 3.7). Within 'other', calling was the most frequent behaviour (50.0 % ± 34.7).

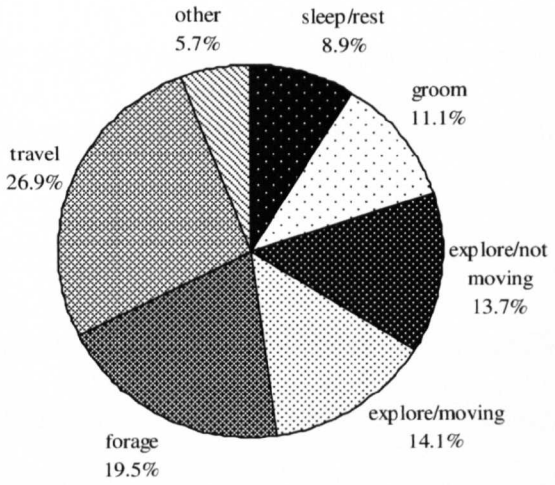


Figure 3.7. Activity budget for radio-collared animals (N= 17, nine males, eight females). 'Other' included the activities calling, urine-marking, and socialising.

Based on our observations, the diet of lorises at MPFR consisted only of insects and small geckos. They were never seen eating fruit, flowers or gum. However, they were seen sucking on bamboo shoots, which may have been a way to drink water or feed on small larvae and insects present inside the small water ecosystem formed within bamboo stems. They were also seen drinking out of small water holes on tree trunks. Lorises caught their prey in several ways. They either did so passively or actively. They adopted a 'sit and wait' approach and grabbed insects walking along a branch or on a leaf nearby or catching flying insects. They alternatively actively searched for food, which involved moving around, often frantically, particularly following a bout of rain, and at times, moving onto the ground to forage for insects under the leaf litter. Lorises foraged by either moving within one small bush, or the canopy of a tall tree, by rapidly climbing up and down lianas to grab prey on the ground, or by actively searching for food on the ground. One of the radio-collared males, MA, was observed grabbing small cockroach-like insects as they came out of a small hole in a thick liana, with one hand or directly with the mouth. The type of insect eaten could almost

never be recorded but insects belonging to the following orders were recognised: Orthoptera, Blattodea, Isoptera, Hymenoptera, Hemiptera and Coleoptera. They also were observed eating larvae and caterpillars and on one occasion a small gecko.

Summary

- The slender loris population in MPFR probably consisted of 29 animals (based on the number of recognised individuals), of which 21 were caught. Sex ratio was 13 males to 12 females. Non-juvenile males are significantly heavier than non-juvenile females. There was no significant difference in body length between males and females. Mean testis size for males corresponds to 3.5 times more than the predicted value based on their weight.
- Lorises were considered completely nocturnal as activity did not start until sunset (between 17.45 and 18.00) and ended between (06.00 and 06.30). Travelling outside the sleeping site did not start until the end of the nautical twilight (18.30 and 18.45) when the night was dark. Slender lorises reached an activity plateau between 19.00 and 20.00. Activity levels remained high until 06.00 at which point lorises would travel back to their sleeping sites. Young lorises (infants, juveniles and subadults) were generally less active throughout the night than adults.
- Lorises were recorded as 'active' (Mean = 75.6 % $\pm$ 11.2), more frequently than 'inactive'. Active periods were dominated by travelling, followed by foraging, exploring whilst moving and grooming. Inactive periods consisted of exploring without moving and resting or sleeping. Within 'other', calling was the most frequent behaviour.
- The diet of lorises consisted only of insects and small geckos, lorises were also seen sucking on bamboo shoots.

3.4. RANGING BEHAVIOUR

3.4.1. Distribution of home ranges across MPFR

The home ranges of all lorises caught (except two juveniles) are illustrated in figure 3.8 to show their position within the forest and in relation to general forest features, such as pine forest plantations, paddy fields, paths and forest edge.

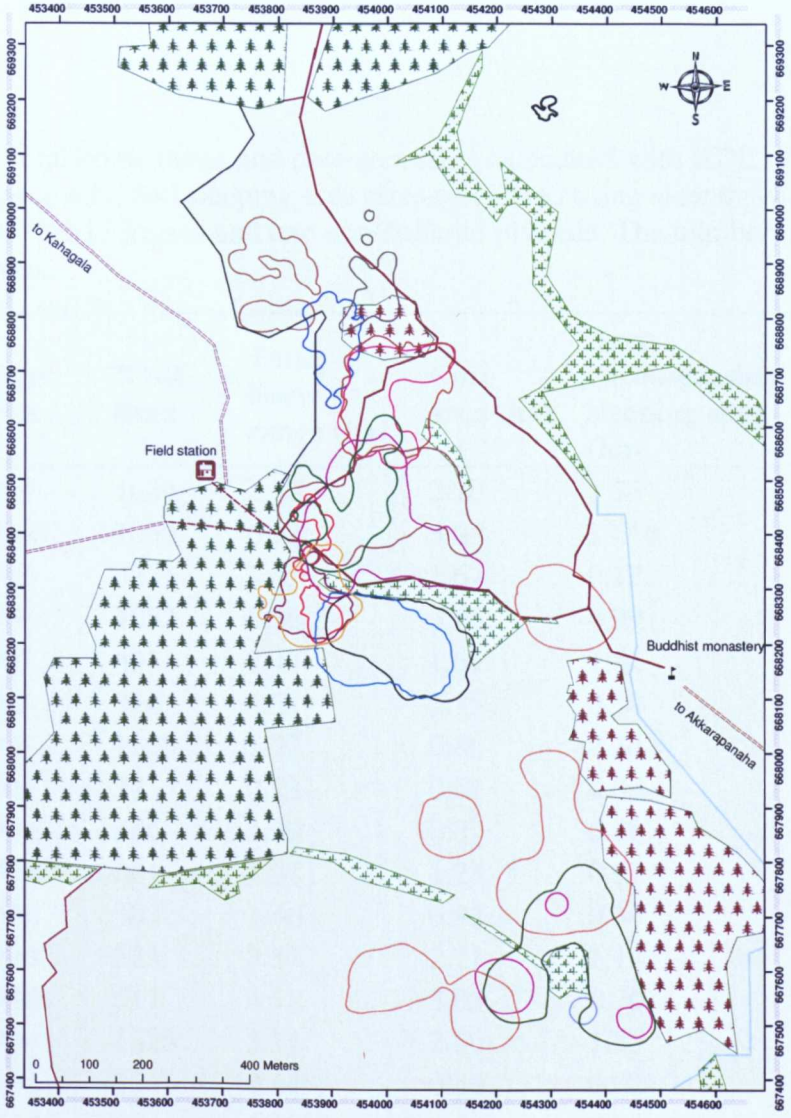


Figure 3.8. Distribution of home ranges of 15 adult lorises (eight males and seven females) and one juvenile within the study site. Each loris has a different colour coded outline. Home ranges were calculated using KDE (95%) (see Section 3.4.2 for exact figures). For a detailed legend of map features refer to Figure 2.5.

3.4.2. Home range and core area size

We radio-tracked 16 adult lorises and one sub-adult loris between August 2005 and July 2006, with an average of 20.7 ± 13.6 track nights and 603.1 ± 506.0 fixes per animal and an average of 19.0 ± 16.0 sleeping sites per individual. Only 13 animals had enough location points and were tracked long enough to obtain a reliable estimate of home range size to be used in further analyses. Nevertheless, the home range sizes obtained for the remaining four animals (three males and one female) are given in table 3.6.

Table 3.6. Total home range and core area sizes calculated with KDE (95%) and KDE (85%), respectively, and sleeping area sizes calculated using sleeping sites only with MCP(100%) for 17 lorises and one non-collared juvenile. The number of core areas also are given.

ID	Age /sex	N° of fixes	Total home range (ha)	Core area (ha)	Area encompassing sleeping sites (ha)	N° of core areas
FB	AF	1639	2.78	2.20	1.33	1
FG	SAF	1059	6.92	3.95	13.16	5
FF	AF	327	2.45	1.67	0.12	2
FI	AF	1057	5.36	3.76	4.99	2
FK	AF	691	2.43	1.67	1.84	2
FM	AF	346	4.51	3.15	0.58	3
FE	AF	1168	1.22	0.86	0.34	1
FR	AF	37	0.73	0.51	0.05	1
MJ	AM	486	1.39	0.87	0.88	1
MH	AM	681	1.91	1.23	0.97	1
MA	AM	303	1.40	0.93	0.34	1
MD	AM	625	3.37	2.71	1.14	1
MO	AM	611	4.12	3.03	0.70	1
MT	AM	1525	3.11	2.50	1.85	1
MC	AM	55	0.64	0.40	0.02	1
Ma	AM	89	1.10	0.48	0.04	1
ML	AM	85	0.55	0.41	0.35	1
JMP	JM	39	0.06	0.04	0.01	1

Home range size was on average 3.15 ha ± 1.70 and core area size 2.19 ha ± 1.08, whilst core area size based on sleeping site locations only and calculated using 100 % MCP, measured an average of 2.17 ha ± 3.53. Slender lorises had between one and five core areas. Female home range size estimated using KDE, ranged between 6.92 hectares and 1.22 hectares whilst male home range size ranged between 3.37 hectares and 1.39 hectares.

There was no significant difference in total home range size between males (Mean = 2.6 ha ± 1.1 and females (Mean = 3.7 ± 2.0) (Student t-test: t = -1.21, d.f. = 11, ns). There also was no significant inter-sexual difference in core area size calculated using KDE (Females: Mean = 2.50 ± 1.20 - Males: Mean = 1.90 ± 1.00) (Student t-test: t = -0.971, d.f. = 11, ns) and in core area size calculated with sleeping sites alone (Females: Mean = 3.19 ± 4.70 - Males: Mean = 1.00 ± 0.51) (Student t-test: t = -1.239, d.f. = 11, ns).

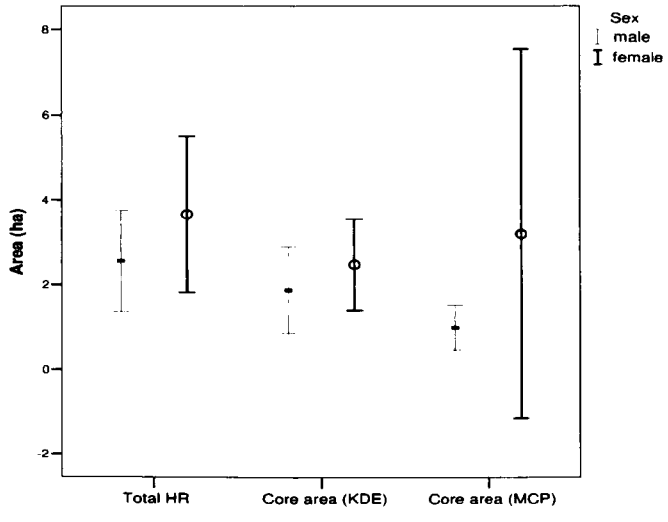


Figure 3.9. Comparison between males (N = 6) and females (N = 7) in mean (± txSE) home range size (total HR calculated using KDE 95%), core area size (core area (KDE) calculated using KDE 85%) and core area size calculated using sleeping site locations only (core area (MCP) calculated using MCP 100%).

Females (N = 7) significantly differed from males (N = 6) in the number of core areas they had (Females: mean = 2.5 $\pm$ 1.3, Males: all had just one core area) (Student t-test = -2.46, d.f. = 11, p = 0.05). One female (FG) had five core areas.

The ranging pattern of a juvenile of approximately one month of age also was determined and represented below to show the rapid increase in home range size from the time it was first followed. For this purpose I used the MCP (100 %) method to show the increase in size as a result of the increasing frequency of occasional sallies from its parking spot (Figure 3.10). The first two nights that the infant was followed, its home range was 0.02 hectares and movements were limited. The following two nights, the home range increased to 0.09 hectares and the infant moved relatively longer distances. Location fixes from the following two nights resulted in a cumulative home range of 0.11 hectares, whilst location fixes from the 18th and 19th of June resulted in a cumulative total home range of 0.12 hectares. This figure remained the same despite more location fixes collected until the 25th of June (Figure 3.10).

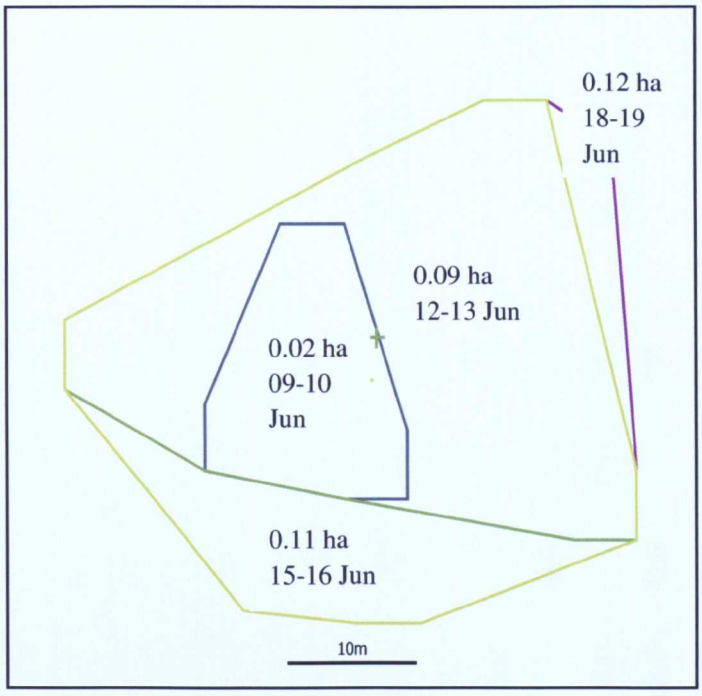


Figure 3.10. Home range of one month old infant Juvenile male (JMP), who was still at the stage of being parked by its mother and picked up before dusk when caught. A total of 39 location fixes were obtained. Home range sizes were calculated using MCP (100%) and illustrated here to show the increase in home range size over a short period of time.

3.4.1. Home range overlap

Overlap was measured as percentage of one total home range overlapping the total home range of another individual. For the purpose of showing overlap between different individuals I included in the analysis one of the males (ML) that I excluded from home range size analysis (due to small sample size). This is because I had recorded ML's presence within FM's home range whilst tracking her and wanted to determine what part of her home range he overlapped. Table 3.7 shows the percentage of overlap between all individuals.

Table 3.7. Home range overlaps between 14 radio-collared individuals (seven females and seven males). The ranges of individuals in column overlap those of individuals in rows. Values in bold depict percentage overlap between males (M) and females (F) (> 10%). Those in red represent female-female overlap (> 10%) and those in blue, male-male overlap (> 10%).

	FB	FG	FF	FI	FK	FM	FE	MJ	ML	MH	MA	MD	MO	MT
FB		0.0	0.0	0.0	0.0	1.9	5.1	0.0	0.0	8.0	0.0	**78.2**	0.0	0.0
FG	0.0		0.0	0.0	0.0	15.5	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
FF	0.0	0.0		54.4	8.0	0.0	0.6	0.1	0.0	4.6	0.0	0.0	**44.3**	8.9
FI	0.0	0.0	43.7		2.5	0.0	0.5	0.0	0.0	5.5	0.0	0.2	**39.6**	1.4
FK	0.0	0.0	16.2	6.2		0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	**88.0**
FM	1.3	24.1	0.0	0.0	0.0		0.0	0.0	9.1	0.0	0.0	0.0	0.0	0.0
FE	12.4	0.0	1.0	2.2	0.0	0.0		0.0	0.0	**84.8**	0.0	10.0	0.0	0.0
MJ	0.0	0.0	0.4	0.0	00	0.0	0.0		0.0	0.0	3.1	0.0	0.0	0.4
ML	0.0	0.0	0.00	0.0	0.0	**81.9**	0.0	0.0		0.0	0.0	0.0	0.0	0.0
MH	**13.2**	0.0	**12.1**	**17.9**	0.0	0.0	**57.7**	0.0	0.0		0.0	11.4	1.7	0.0
MA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0		0.0	0.0	0.0
MD	**63.9**	0.0	0.0	0.3	0.0	0.0	3.4	0.0	0.0	5.6	0.0		0.0	0.0
MO	0.0	0.0	**50.8**	**56.5**	0.6	0.0	0.0	0.0	0.0	0.8	0.0	0.0		0.0
MT	0.0	0.0	**12.1**	2.4	**59.1**	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	

3.4.2. Inter- and intra-sexual overlap

Amongst the radio-collared individuals, there appeared to be four males that shared a large proportion of their home ranges with an adult female: MO-FI, MT - FK, MD – FB and MH - FE (Figure 3.11). Each male whose home range coincided with a female's home range, also overlapped part of another female's home range but only by 10 % or less. One exception was MO whose home range overlapped that of two females, FF and FI, who shared > 50 % of each other's home range.

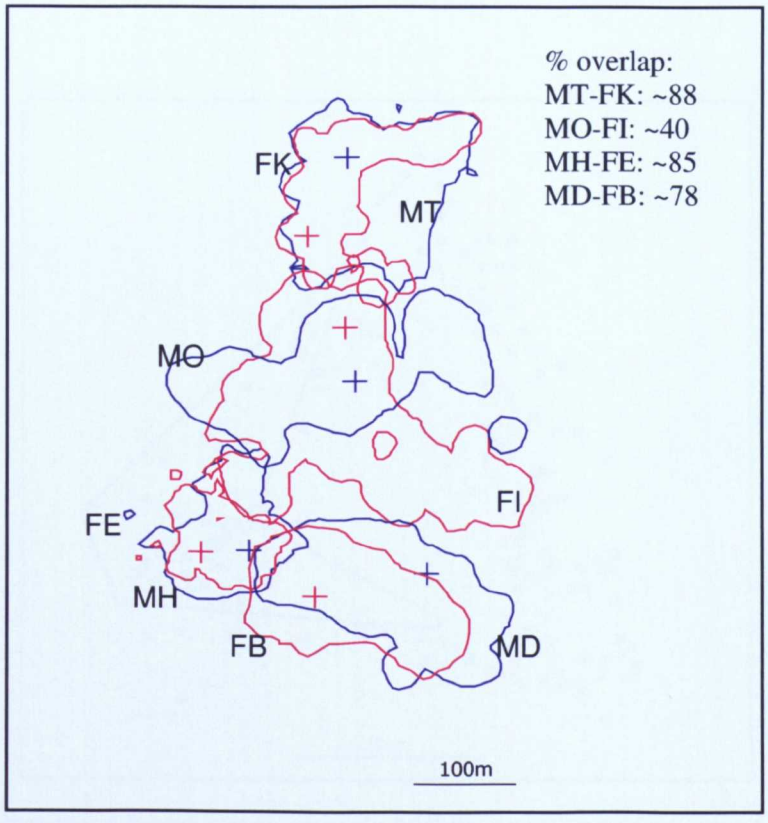


Figure 3.11. Patterns of home range overlap between four male-female pairs: FK and MT; FI and MO; FE and MH and MD and FB. Red lines represent female home ranges, and blue lines represent male home ranges.

Due to differences in home range size, females sometimes overlapped a larger proportion of the male's home range and vice-versa. For example, female FI overlapped about 57 % of male MO's home range. MO's home range however overlapped only approximately 40 % of FI's home range. In the case of female FM and male ML, the female's home range overlapped the male's home range considerably more (~ 82 % against ~ 9 %). This is due to the fact that ML's home range estimate is based on too few location fixes, resulting in a smaller home range area than was probably the case. In order to see the potential extent of ML's home range, and thus the potential extent of overlap between these two animals, I estimated his home range using the MCP (100 %) method (Figure 3.12).

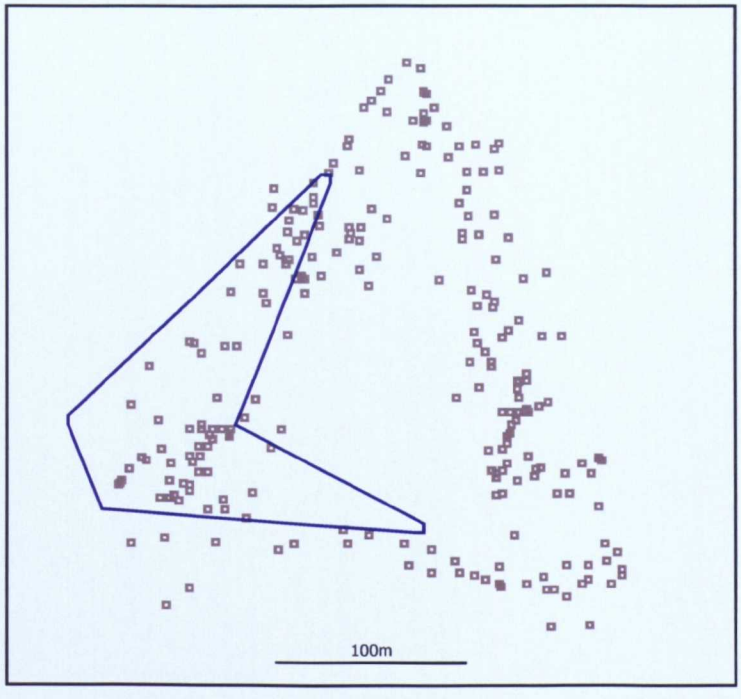


Figure 3.12. Presumed home range of male ML by using the Minimum Concave Polygon method at 100%. The blue line encompasses ML's home range. The grey points represent location fixes for both ML and FM. ML's home range covers about 20% of FM's when all points are included in the analysis.

The home range estimated using KDE at 95 % was 0.40 hectares. When using the 100% MCP method, the home range of ML increased to about 2.20 hectares, an estimate well within the range of a male's mean home range. This results in a potential overlap with FM, of 20 %, as opposed to 9 % (Figure 3.12). The female FM's home range still overlapped that of ML's considerably more and it may simply be that ML's home range was much larger than was estimated here, even using the 100 % MCP method.

The highest overlapping ranges between females occurred between females FM and FG (FG's home range overlapped that of FM's by 24 %) and females FB and FE (FB's home range overlapped that of FE's by 12 %). Other home range overlaps are below 10 % (Figure 3.13). Amongst males, there was little overlap (< 10 %), except between MD and MH (11.4 %) (Figure 3.14).

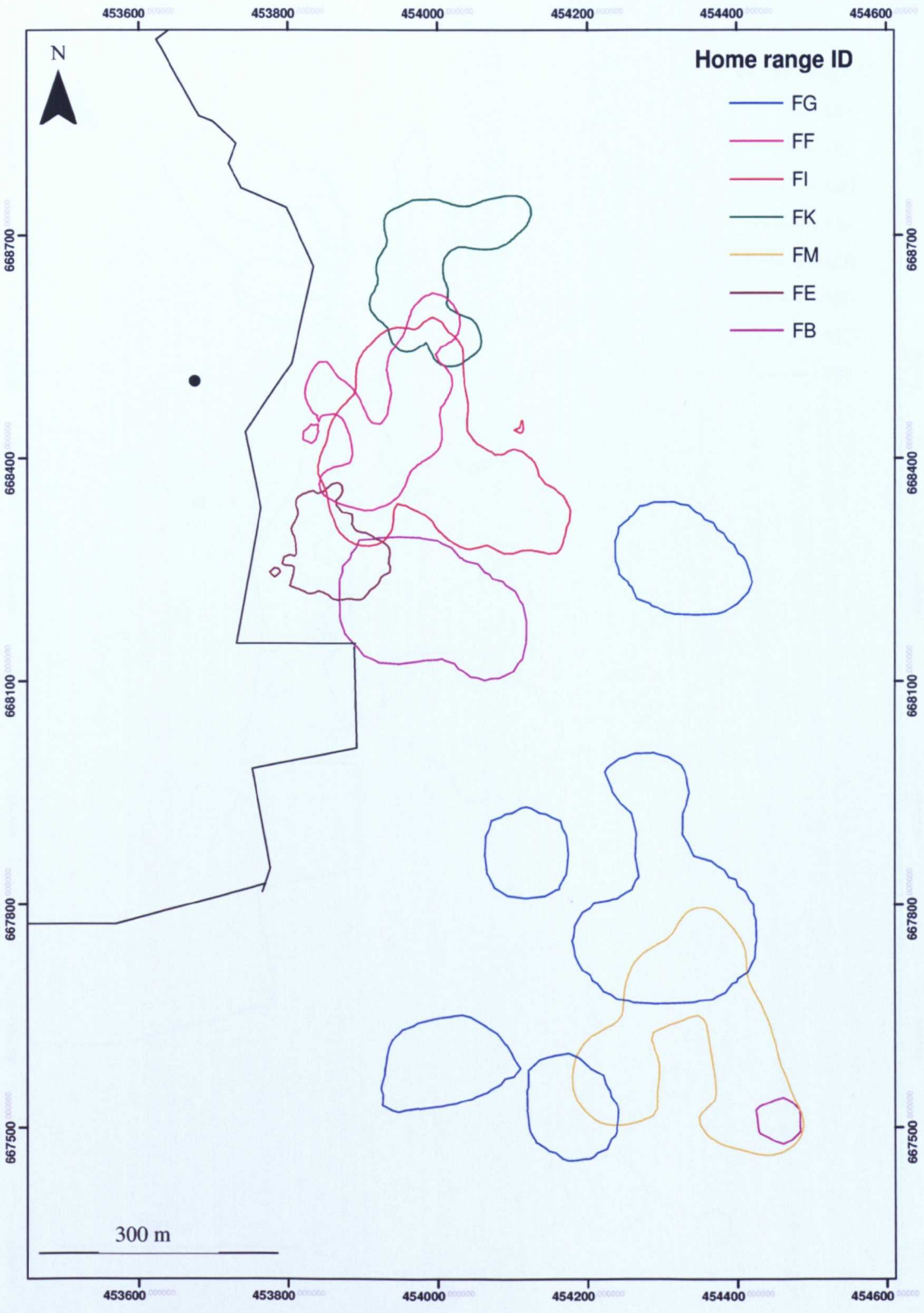


Figure 3.13. Home range overlaps between seven females. Different coloured lines represent the home ranges of different individual females (calculated with KDE). The forest edge is represented by the black line and the study station by the black dot.

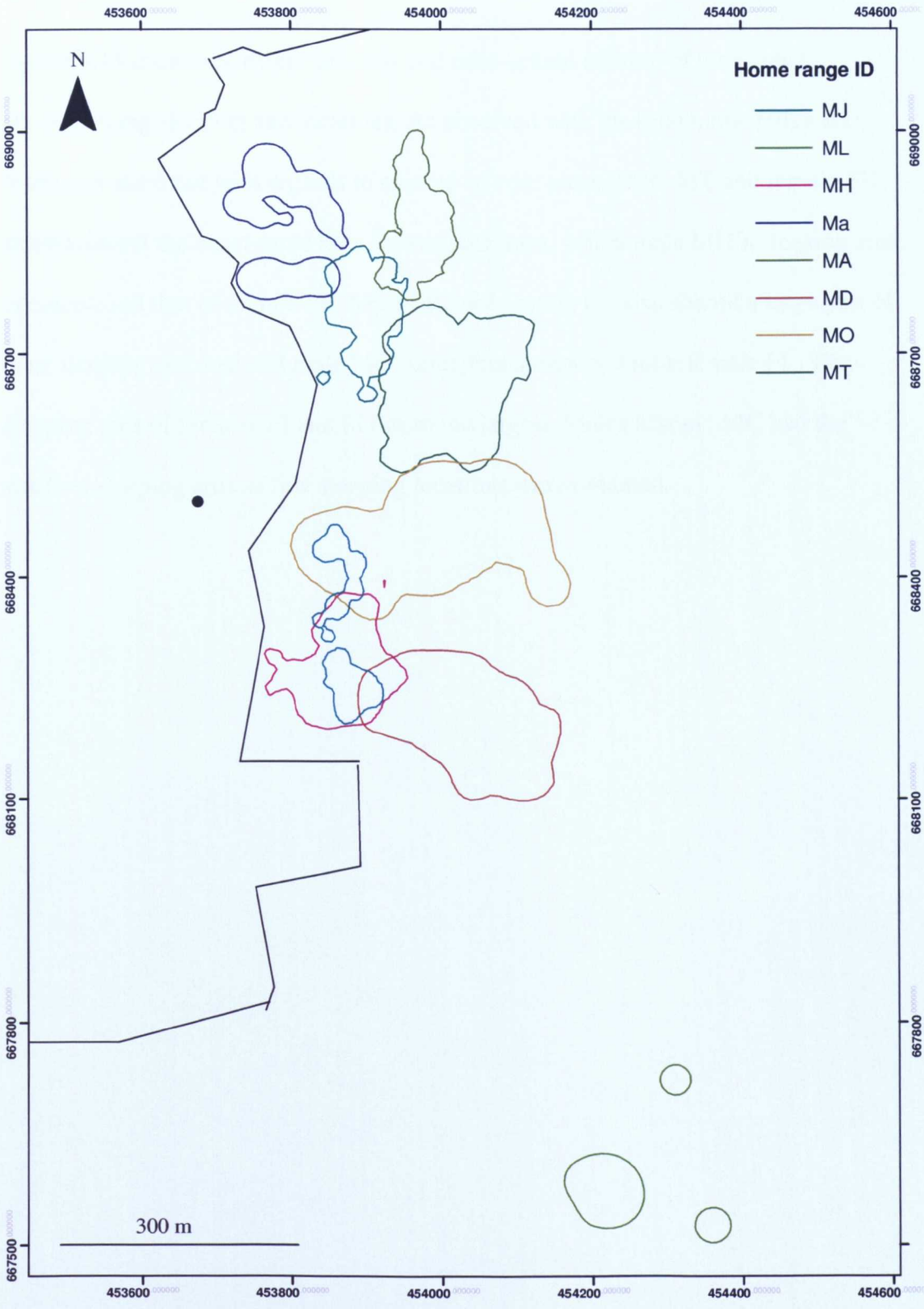


Figure 3.14. Home range overlaps between eight males. Different coloured lines represent the home ranges of different individual males (calculated with KDE). The forest edge is represented by the black line and the study station by the black dot.

3.4.5. Overlap of sleeping site areas

Figure 3.15 shows the extent of inter- and intra-sexual overlap of core areas encompassing sleeping site locations. As observed with the total home range area, four pairs stand out with regards to overlap of core areas. Male MT and female FK shared almost the exact same area for sleeping sites, whilst male MH's sleeping area encompassed that of female FE. Male MD and female FB also shared a large part of their sleeping site area and male MO's sleeping area was within female FI. The sleeping area of females FI and FG were the largest. Males Ma and MC had the smallest sleeping area as few sleeping locations were obtained.

Figure 3.15. Overlap of sleeping areas calculated using sleeping site locations of each individual (using MCP). Different coloured polygons reflect a different animal with the ID of the animal distinguishing each core area.

3.4.6. Summary of home range overlap

Inter-sexual overlap was significantly higher (Mean = 28.5 % ± 32.8) than intra-sexual overlap (Mean = 5.4 % ± 6.5) (Student t-test = 3.36, d.f. = 40, p = 0.002). This relationship held true whether or not the overlapping percentage between ML and FM was changed to the predicted value based on ML's home range (Student t-test = 3.45, d.f. = 40, p = 0.002) (Figure 3.16)

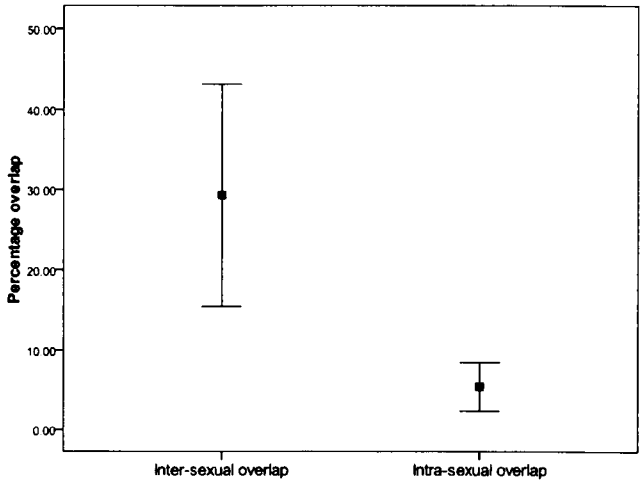


Figure 3.16. Inter-sexual difference in mean (± 2SE) percentage overlap.

Female-female overlap was on average higher (Mean = 7.2 % ± 7.8) than male-male overlap (Mean = 3.2 % ± 3.8) although the difference was not significant (Student t-test = 1.31, d.f. = 16, p = 0.21) (Figure 3.17).

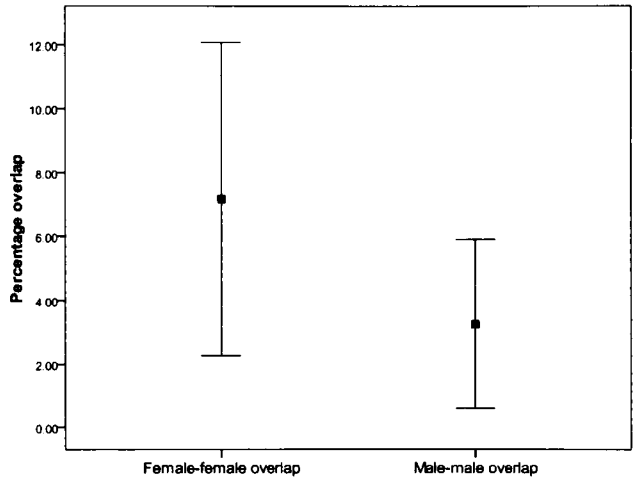


Figure 3.17. Difference in mean (± 2SE) percentage overlap between females and between males.

Although, the number of female-female home ranges overlapping was slightly higher (Mean = 1.7 ± 0.5) than the number of male-male overlapping home ranges (Mean = 1.1 ± 0.7) the difference was not significant (Student t-test = 1.53, d.f. = 11, p = 0.16).

Females overlapped an average of 1.5 ± 1.1 male home ranges and males overlapped an average of 1.7 ± 0.9 female home ranges.

3.4.7. Nightly path length and home range defendability

I calculated three indices of home range defendability and average path length (Table 3.8) to assess the ability of individual lorises to defend their home ranges and assess whether home ranges could be described as defendable territories rather than home ranges (Morse, 1980).

Table 3.8. Indices of home range defendability for 12 of the radio-collared lorises at MPFR (five males and seven females). In this table d' = diameter of home range; d = mean nightly path length (km); C = circumference of home range; D = index of defendability (Mitani and Rodman, 1979); RTI = range traversing index (Martin, 1981); M = fractional monitoring index (Lowen and Dunbar, 1994).

ID	d'	D	C	D	RTI	M
FK	0.2	1.6	0.6	9.4	2.9	5.5
FE	0.1	1.5	0.4	11.6	3.7	5.3
FB	0.2	1.4	0.5	8.6	2.7	4.9
FF	0.2	1.3	0.5	7.4	2.4	4.6
FI	0.2	1.3	0.6	6.6	2.1	3.1
FM	0.2	1.1	0.6	5.7	1.8	1.6
FG	0.3	0.9	0.9	3.1	1.0	0.6
MJ	0.1	1.4	0.5	9.4	3.0	6.0
MD	0.2	1.5	0.5	8.8	2.8	4.9
MH	0.1	1.3	0.5	8.8	2.8	4.5
MO	0.2	1.3	0.6	7.2	2.3	3.8
MT	0.2	1.6	0.7	7.6	2.4	2.3

Lorises at MPFR travelled an average of 1346.0 $\pm$ 511.3 m/night with a maximum of 2995.0 metres in one night in March by male MT and a minimum of 301.0 metres also in March by female FG. Lorises travelled an average of 112.2 $\pm$ 42.6 m/hr with a maximum of 250.0 m/hr by male MT, and a minimum of 25.0 m/h by female FG. There were no significant inter-sexual differences in mean nightly and mean hourly distance (Table 3.9).

The index of defendability (D) was greater than one for all lorises and a mean of 7.9 $\pm$ 2.2 and ranged from an index of 3.1 for subadult female FG to 11.6 for adult female FE. This demonstrates that all lorises at MPFR, even FG who had the smallest mean path length and largest home range, were able to traverse their home ranges in one night. The range traversing index (RTI) was greater than '1' for all lorises except FG

(= 1.0) (N = 12, mean = 2.5 ± 0.7; range: 1.0 to 3.7). This suggests that all lorises at MPFR, except FG, were able to travel the circumference of their entire home range in one night. Even in the case of FG, this would have been possible as her RTI value was 1.0. The fraction monitoring index (M) was greater than '1' for all lorises except FG (0.6) (N = 12, mean = 3.9 ± 1.7) with adult male MJ having the highest M value (6.0). The fraction monitoring index, which takes into account the number of independently moving groups surrounding the individual's home range, and detection distance (Lowen and Dunbar, 1994), suggests that all lorises at MPFR, except the subadult female FG, were capable of defending their home range from surrounding individuals. There were no significant differences in range defendability between males or females (Table 3.9).

Table 3.9. Analysis of inter-sexual differences in mean (± SD) (range in brackets) path length and defendability indices, for five males and seven females using the Student t-test. D = Index of defendability; RTI = Range Traversing Index and M = Fraction Monitoring Index.

	Mean path Length (km)	**D**	**RTI**	**M**
Males (5)	1.40 ± 0.13 (1.30 – 1.60)	8.4 ± 0.9 (7.2 – 9.4)	2.7 ± 0.3 (2.3 – 3.0)	4.3 ± 1.4 (2.3 – 6.0)
Females (7)	1.32 ± 2.40 (0.90 – 1.60)	7.5 ± 2.7 (3.1 – 11.6)	2.4 ± 0.9 (1.0 – 3.7)	3.7 ± 1.9 (0.5 – 5.5)
T	0.73	0.70	0.70	0.61
d.f.	10	10	10	10
P	0.48	0.50	0.50	0.56

Summary

- We radio-tracked 16 adult lorises and one sub-adult loris between August 2005 and July 2006. Average home range size for lorises was 3.15 ha $\pm$ 1.70 and core area size 2.19 ha $\pm$ 1.08, calculated using the KDE method (95% and 85% respectively). The average area encompassed by 100% of sleeping site locations measured 2.17 ha $\pm$ 3.53 using the MCP method. There was no significant inter-sexual difference in total home range size (KDE), core area size (KDE) and core area size (sleeping sites only). Females had between one and five core areas within their home ranges whilst males only had one.
- Inter-sexual overlap was significantly higher than intra-sexual overlap. Overlap was extensive (> 50 % on average) only with one other animal (of the opposite sex) whilst overlap with any other animals was significantly lower (< 15 % on average). There was no significant difference between extent of female-female and male-male overlap (Figure 3.17).

- Lorises at MPFR travelled an average of 1346.0 $\pm$ 511.3 m/night and 112.2 $\pm$ 42.6 m/hr. The index of defendability (D) was greater than one for all lorises. The range traversing index (RTI) and fraction monitoring index (M) were greater than one for all lorises except the subadult female FG. There were no inter-sexual differences in range defendability indices.

3.5. SOCIAL BEHAVIOUR

3.5.1. Sociality throughout the night and according to activity

Adult slender lorises at MPFR, including non-collared ones, were within 30 metres of other lorises 21.4 % of observations, within 20 metres, 18.0 % of observations, within 10 metres, 9.6 % of observations, and within five metres, 6.2 % of observations. In 87.9 % of observations, a loris was within 30 metres of just one other loris, whilst it was recorded to be within 30 metres of two other lorises, in 9.2 % of observations, and in the presence of another three lorises in 2.9 % of observations. Percentage sociality differed significantly across the night with the majority of social interactions occurring in the early hours and late hours of the night (Friedman test: Chi-square = 20.7; d.f. = 12; p = 0.05). However, lorises were social at all hours of the night (Figure 3.18).

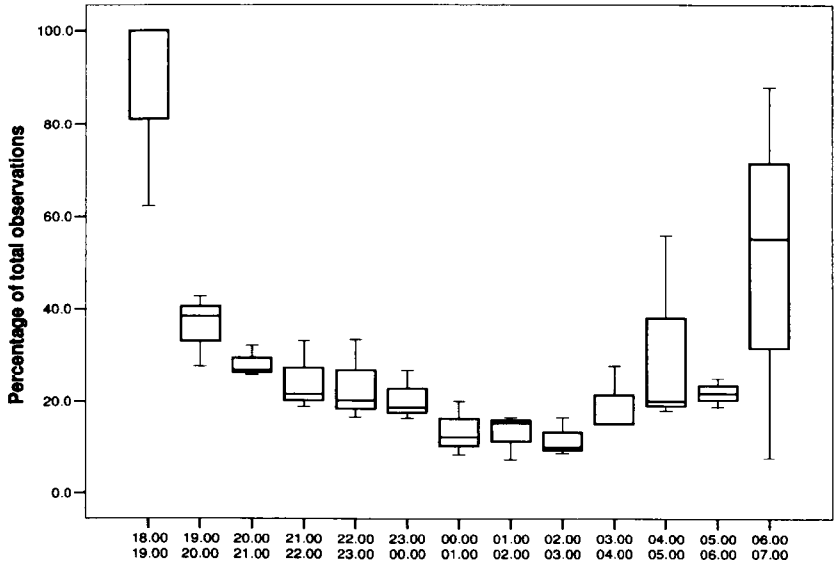


Figure 3.18. Percentage of total observations that lorises (N = 12) were recorded within 30 metres of another loris in each hour of a 13 hour night, between 18.00 and 07.00.

Inter-individual distance significantly varied according to time of night (Table 3.10) (Figure 3.19).

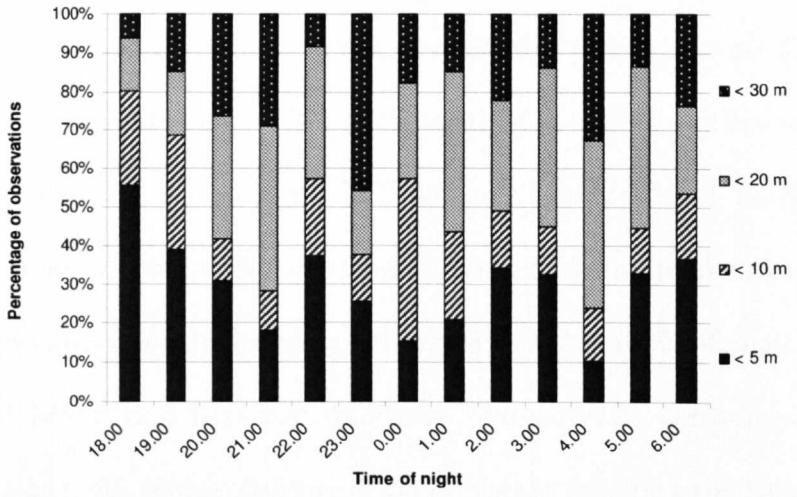


Figure 3.19. Inter-individual distance (IID) recorded between lorises (N = 12) in each hour of the night.

Table 3.10. Results of Friedman test looking at difference with which lorises (N = 12) were within different IIDs throughout the night.

IID	< 5 m	10 m – 20 m	20 m – 30 m	20 m – 30 m
Chi-square	28.44	27.64	30.90	31.24
d.f.	12	12	12	12
P	0.005	0.006	0.002	0.002

Lorises were mostly within five meters of each other between 18.00 and 19.00 (Median = 33.3%, IQ Range = 73.4, Min = 2.0, Max = 100.0) and between 06.00 and 07.00 (Median = 28.0%, IQ Range = 31.9, Min = 5.5, Max = 53.3) but were observed within five metres of another individual relatively frequently at other times of the night. For distances between five and 10 metres lorises also showed significant differences throughout the night. They were mostly within these distances of another

loris between 19.00 and 20.00 (Median = 50.0, IQ range = 41.9, Min = 5.9, Max = 100.0) and between 00.00 and 01.00 (42.3, 39.8, Min = 11.6, Max = 70.00). Significance also was found for distance between 10 metres and 20 metres with lorises being mostly observed at these distances of other lorises between 21.00 and 22.00 (Median = 28.9, IQ range = 31.5, Min = 5.0, Max = 50.0) and between 04.00 and 05.00 (Median = 28.9, IQ range = 35.2, Min = 9.1, Max = 55.0). Lorises were within 30 metres of other individuals at significantly different frequencies throughout the night with most observations being between 23.00 and 00.00 (Median = 28.9, IQ Range = 46.2, Min = 12.0, Max = 85.0). Figure 3.20 shows the percentage of different behavioural categories observed during focal follows in relation to distance of focal animal to other conspecifics.

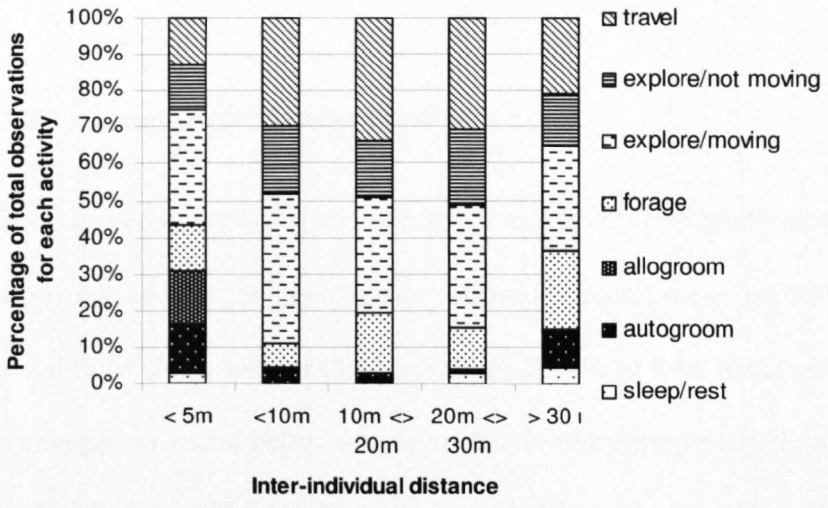


Figure 3.20. Percentage of different behaviours according to distance between the focal loris and another loris (N = 12). Distances range from within five metres to beyond 30 metres.

Apart from the 'exploring' behaviours (with or without movement), all other behaviours occurred at significantly different frequencies depending on inter-individual distance (Table 3.11). Thus, travelling was mostly recorded when IID was

between 10 and 20 metres (Median = 42.9, IQ range = 35.0, Range = 0.0 – 100.0), foraging occurred mostly at IIDs of > 30 metres (Median = 11.5, IQ range = 13.5, Range = 0.0 – 100.0), autogrooming occurred mostly at IIDs of < 5 metres (Median = 6.3, IQ range = 23.5, Range = 0.0 – 60.0) and sleeping/resting occurred mostly at IIDs of > 30 metres (Median = 6.0, IQ range = 15.0, Range = 0.0 – 25.4).

Table 3.11. Results of Friedman test looking at difference in percentage of observations of different behavioural activities according to inter-individual distance for the twelve individuals.

Behaviours	**Travel**	**Explore/ NM**	**Explore/ M**	**Forage**	**Allo-groom**	**Auto-groom**	**Sleep/ rest**
Chi-square	10.55	1.80	8.77	11.28	26.02	17.28	20.20
d.f.	4	4	4	4	4	4	4
P	0.03	0.77	0.07	0.02	< 0.01	< 0.01	< 0.01

3.5.2. Social contacts between adults

Table 3.12 shows percentage of total observations radio-collared individuals engaged in social behaviour and percentage of observations for each type of social behaviour. Radio-collared individuals were social on average 29.2% of total observations (N = 16). Males engaged in social behaviour significantly more frequently than females (Males: N = 8; Median = 28.5 % - Females: N = 8; Median = 21.4 %) (MWU: 10.0, $n_1 = 8$, $n_2 = 8$, $z = -2.083$, $p = 0.04$). Neutral interactions made up the largest proportion (52.1 %) of interactions for the whole population, followed by positive and indirect interactions (32.8 %). Negative and direct interactions such as fighting were rare making up 0.4 % of total observations. Positive and direct interactions such as allogrooming and playing were more frequent making up 9.6 % of total observations (Table 3.12). In some cases I collected less than 50 sample points (20 hrs) of data on

an individual. This was the case for three of the radio-collared animals. Thus, I conducted the same statistical tests by removing these animals from analysis and the results remained the same, with males being significantly more social than females.

Table 3.12. Percentage sociality according to different categories of social behaviour: direct positive, direct negative, indirect positive, indirect negative and neutral. Values in the last row represent the mean percentage (of total observations) for different categories of social interactions (direct, indirect, positive, negative, and neutral).

ID (N)	% social	%direct positive	%direct negative	%indirect positive	%indirect negative	%neutral
FF (262)	19.5	0.0	0.0	14.3	0.0	85.7
FE (969)	19.9	12.8	0.0	38.1	0.0	49.2
FB (987)	24.2	10.5	0.9	40.2	0.0	48.4
FI (758)	17.8	1.1	0.0	20.7	5.4	72.8
FG (572)	4.0	0.0	0.0	31.6	21.1	47.4
FK (386)	35.2	14.4	0.0	70.0	0.0	15.6
FM (489)	24.3	1.1	0.0	14.8	5.7	78.4
FR (50)	9.8	0.0	0.0	100.0	0.0	0.0
MJ (71)	60.6	9.2	0.0	18.1	18.2	54.5
MA(113)	70.8	0.0	7.7	23.1	23.1	46.2
MD (177)	40.7	13.3	0.0	50.0	0.0	36.7
MT (1057)	20.1	8.3	0.0	40.9	1.7	49.2
MC (25)	28.0	5.8	0.0	22.7	0.0	71.5
MH (256)	18.4	15.0	0.0	22.3	0.0	62.7
MO (436)	26.8	1.7	0.0	18.3	4.3	75.7
ML (15)	46.7	60.0	0.0	0.0	0.0	40.0
Total n = 6624	29.2	9.6	0.4	32.8	3.5	52.1

In section 3.2.3 I demonstrated that five male-female pairs shared extensive parts of their home ranges. I examined sociality between members of a pair (Table 3.13). Positive interactions only occurred between individuals with extensive home range overlap and consisted of individuals allogrooming, playing and moving together, both at the sleeping site and throughout the night. Little negative interactions occurred between individuals in general. Most were observed between female FM and females

FG and FB. The latter two attempted to move within FM's home range. No interactions were ever observed between FB and FG whose home ranges remained separate. The other negative interactions observed occurred between neighbouring males and females such as female FE and male MT. Interactions appeared to be territorial with MT trying to move into FE's home range. Negative interactions were never direct and were always accompanied by exchanges of whistles.

Table 3.13. Social contacts exhibited by members of a radio-collared pair towards other collared and non-collared lorises (values represent percentage of total observations between individuals)

Pair	**% Social contact exhibited by female to paired male**	**% Social contact exhibited by female to other individual(s)**	**% Social contact exhibited by male to paired female**	**% Social contact exhibited by male to other individual(s)**
FB MD	59: 60.3 positive 39.7 neutral	10.0 – FM 24.0 - two UIs	75.0: 60.9 positive 36.9 neutral	18.0 – UF 7.0 - UI
FE MH	70.8: 43.5 positive 56.5 neutral	22.6 - MC 6.0 - UI	98.0: 38.0 positive 62.0 neutral	2.0 - MO
FK MT	90: 84.4 positive 15.6 neutral	6.0 - FI 4.0 - UI	76.0: 50.3 positive 46.0 neutral	14.5 - UI 6.0 - FF
FI MO	27: 36 positive 64 neutral	17.0 - UI 14.0- FE 14.0 - FK 14.0 - MT 13.0 – MH	0	44.0 - MH 26.5 - MT 12.8 - FK 16.9 – UI
FM ML	37.6: 59.6 positive 40.4 neutral	43.2 - UI 19.2 – FB	85.7: 50.0 positive 33.0 neutral	14.0 - FG

UI = unidentified individual; UF = unidentified female, M = unidentified male

Interactions between neighbouring males were always indirect and either neutral or negative. Male MJ was observed interacting neutrally with one of the neighbouring males, Ma on three separate occasions along their home range boundaries. No direct interactions occurred, no calls were exchanged and they appeared to tolerate each other's presence. The same relationship appeared to exist between MO and MH and between MO and MT, as both individuals in both cases ignored and tolerated each other, even if within 10 metres of each other. Interactions between MJ and MT and MJ and MA however were different. Both males MA and MT attempted to encroach into MJ's home range and were met by a series of calls from MJ and rapid locomotion towards and along his home range boundary. The intruding males MT and MA responded by retreating rapidly without a vocal exchange taking place. When males were beyond 30 metres from MJ's home range boundary, no negative interactions occurred. Interactions between females were rarely observed except those described earlier. Prior to her dispersal female FB and neighbouring female FE shared about nine per cent of each other's home range and were often within 30 metres of each other without apparent territorial behaviour. On the night that FB was in oestrous a lot of whistle calls were exchanged, some of which appeared to be from female FE who remained within 30 metres of the hub of activity for the first hour or so and then moved off.

In cases where a male appeared to be sharing its home range with a female but was never seen sharing her sleeping site (male MA and a female with a juvenile), direct contact between the male and the female was never positive and consisted of the male attempting to groom the female who aggressively rejected the advances. This was observed only between these two animals on several occasions (16 events over four

nights in August 2005). MA appeared to be sharing part of the female's home range but since she was not radio-collared, spatial analyses cannot confirm this.

3.5.3. Social contacts between adults and infants/juveniles

The lack of visibility coupled with the cryptic behaviour of lorises and their young made observations of adult/young interactions difficult. As a result little data on such interactions are available. Nevertheless, of all interactions observed (N = 23), 100 per cent were between mother and young, 40 per cent of which also occurred in the presence of a male. The majority of such interactions (30 per cent of 23 interactions observed) were initiated by male MA whose home range seemed to overlap at least part of the female's home range and was observed sleeping within 20 metres on two occasions. On two separate nights, MA attempted to initiate contact with the mother and the juvenile, but was aggressively pushed away by the mother both physically and vocally.

Male MJ shared his sleeping site with two other lorises including a female and what was believed to be a young subadult or juvenile based on its size and appearance. MJ interacted with the young by grooming it at the sleeping site until night fell. The young loris and the female remained behind and carried on grooming.

When female FB gave birth, she soon dispersed from the home range she had shared with the male MD and thus no interactions between the latter and the infant were observed.

On one occasion male MT was seen within 20 metres of one of the caught juveniles who was within MT's and FK's home range. MT appeared agitated and moved rapidly back and forth. The juvenile did not react and carried on foraging. It is

difficult to interpret such behaviour without further behavioural data, particularly as that same night we were trying to catch MT to remove his collar and thus his reactions may have been a result of our change in behaviour, which MT would have detected potentially as threatening.

3.5.4. Degree of contact between individuals: Cole's Index of association

Figure 3.21 illustrates the degree of association between radio-collared animals who were observed to interact at some point during their tracking period. This figure shows the approximate position of each individual across the study site (not to scale) and in relation to each other (except individuals for whom not enough social interactions were observed to calculate Cole's index, i.e. males MJ, MA and Ma). Lines between each individual represent Cole's index of association, with the thicker the line the stronger the association.

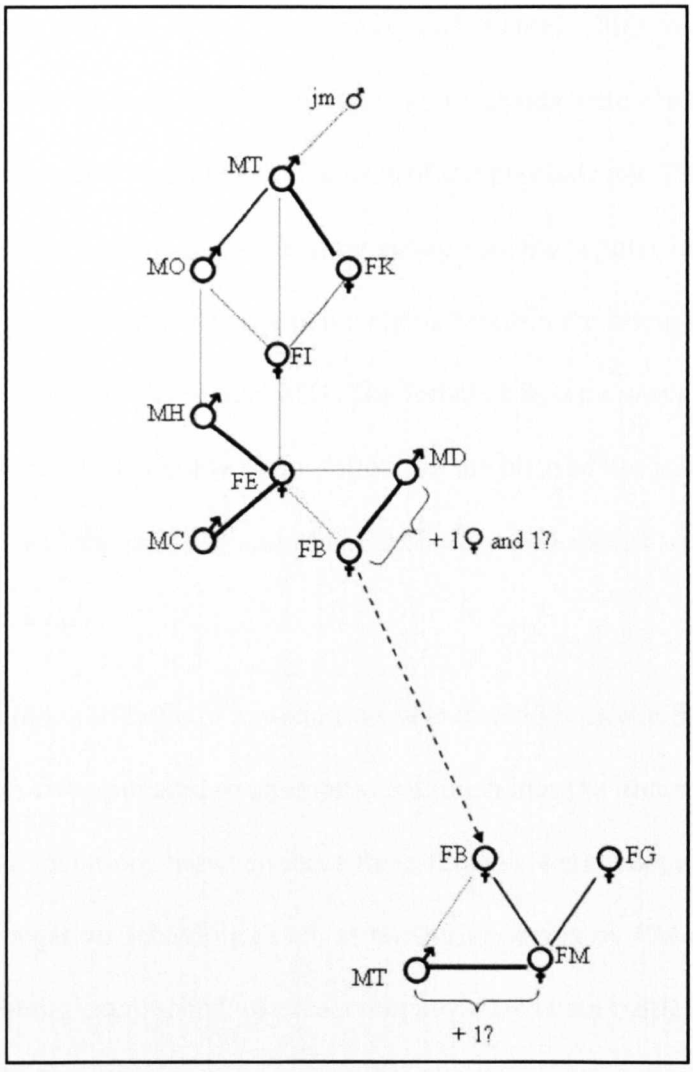


Figure 3.21. Schematic representation (sociogram) of associations between 13 radio-collared lorises and four other (non-collared) lorises. It shows the approximate position of the group and in one case, the dispersal of female FB (represented by dashed arrow line) to an area occupied by a different group The different lines represent the degree of association based on Cole's Index values. The thin line represents association with the smallest index value (< 0.05), followed by the thicker line representing associations with an index value between 0.05 and below 0.5. The thickest line represents associations with index values above 0.5.

Strong associations were found only between males and females, and always between only one male and one female. One female, FE, is shown to have a strong association with two males, but this was not at the same time. One of the males, MC, disappeared from his home range, which he shared with FE. Following its disappearance, another male, MH, moved into the area and built a relationship with FE. Males and females

also had encounters with neighbouring animals, such as male, MO, who also associated with male MH and female FI. These associations were always neutral and no direct interactions ever occurred. In the case of the pair MD and FB, another two individuals were once sighted in the sleeping group and one regular individual, thought to be a female or an immature male, sighted within the home range of this pair and often close to FB rather than MD. The female FB, who was nulliparous when caught, dispersed out of this home range following the birth of her infant, and closer to the home ranges of the pair FM and MT, which they also shared with one other unidentified individual.

In this new situation, a triangle of associations was formed between females FM, FB and FG. The latter two appeared to attempt to encroach into the home range of the former and thus associations between these three females were frequent. There were most frequently negative behaviours such as territorial pacing by FM along the home range boundary being encroached, often accompanied by vocal battles between females FB and FM, or resulting in female FG moving away from female FM. In other cases, particularly after negative interactions had occurred, the females would remain beyond the boundary but within 30 metres of female FM and interactions were neutral.

Cole's Index of association was significantly higher between individuals that were paired (N = 12; Median = 0.79) than between individuals that were unpaired (N = 6; Median = 0.03) (MWU = 0.0, n 1 = 12, n 2 = 6, z = -2.9, p = 0.004) (Figure 3.22).

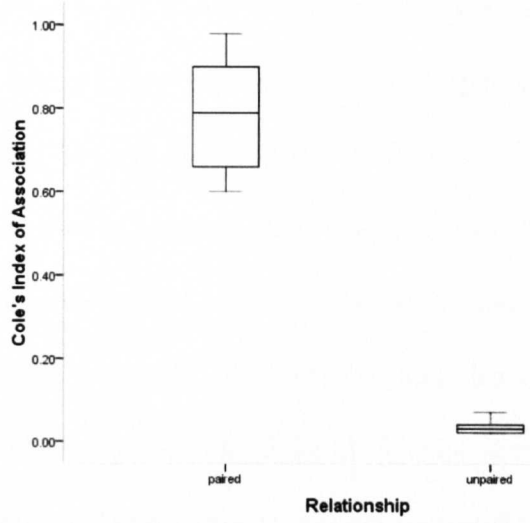


Figure 3.22. Comparison of Cole's Index of association between paired animals (N = 12) and unpaired individuals (N = 6). The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

The sample size was too small to test for differences between female-female and male-male degree of association. The average index of association shows that the degree of association between females (Mean = 0.04 $\pm$ 0.04) was lower than the degree of association between males (Mean = 0.15 $\pm$ 0.06).

3.5.5. Cohesiveness: Jacob's index of association

Analysis of home range overlap between individuals at MPFR revealed four pairs. This is based on the fact that their home ranges overlapped by more than 40%. As described in section 2.6.4, I set out to measure the degree of dynamic interactions between all possible dyads of slender lorises based on Jacob's Index values calculated using Ranges 7 (these values reflect whether movements of two animals indicated attraction, avoidance or indifference) (Table 3.14). Of the four pairs whose home ranges coincided (FE and MH, FB and MD, FK and MT and FI and MO), only two

show high values approaching 1.0 (> 0.7), FK and MT and FB and MD. The pair FM and ML, showed the highest degree of cohesiveness despite showing a smaller degree of home range overlap. This was possibly as a result of too few locations obtained on the male ML, resulting thus in an inaccurate representation of overlap. Nevertheless, ML and FM appear to have formed a pair, both spatially and socially. Despite sharing a large part of their home ranges, FI and MO show an index value of 0.00 suggesting indifference to each other's movements. FE and MC also show high levels of cohesiveness (0.78) but MC's home range was not represented here as too few location fixes were collected to obtain a reliable estimate of home range size. MC disappeared soon after being caught but was replaced by another male (MH) who became FE's spatial partner. Despite MH overlapping ~85% of FE's home range, it does not show as high a level of cohesiveness as that between FE and the previous male MC. Although the female FF and the male MO shared part of each other's home ranges (over 40 %), they were not tracked simultaneously due to the fact that FF disappeared before MO was caught. Thus, an index of cohesiveness could not be calculated for this dyad. No negative value (< 0) was obtained for any of the inter-sexual dyads. Looking at intra-sexual dyads, two male-male dyads (MH-MO and MJ-MT) and one female-female dyad (FB-FM) showed positive degrees of cohesiveness. Apart from the female-female dyad, FK-FI, who showed slight tendency towards avoidance, the other intra-sexual dyads moved independently of each other.

Table 3.14. Dynamic interactions between animals whose home ranges overlapped as indicated by Jacob's Index (-1 to +1). Numbers in italics show a degree of cohesiveness higher than 0.10. Values approaching 1.0 indicate the animals were attracted to each other, while values approaching -1.0 indicate mutual avoidance, and 0 implies indifference.

Inter-sexual dyads	**Jacob's Index of cohesiveness**	**Intra-sexual dyads**	**Jacob's Index of cohesiveness**
FM and ML	*0.98*	MH and MO	*0.44*
FB and MD	*0.89*	MJ and MT	*0.30*
FE and MC	*0.78*	MJ and MA	0.09
FK and MT	*0.70*	MH and MD	0.00
FE and MH	*0.31*	FB and FM	0.36
FF and MT	0.07	FE and FB	0.03
FE and MD	0.03	FG and FM	0.00
FI and MD	0.01	FI and FE	0.00
FF and MJ	0.00	FK and FI	-0.03
FI and MO	0.00		
FB and MH	0.00		
FI and MH	0.00		
FI and MT	0.00		
FK and MO	0.00		

3.5.6. Sleeping associations

The majority of sleeping groups were of two individuals, a male and a female, but in some cases groups consisted of three or four animals. Animals slept either alone, within 20 metres of another sleeping group or in close proximity (huddled) of other individuals. Slender lorises did not use tree holes or nests and instead used tangles of vegetation, lianas and/or vines. Females that were part of a sleeping group were always the first to settle down before sunrise, followed by the associated male. The male would either settle in close proximity to the female or within 20 metres. In the case of FB and MD, another two lorises were observed sharing their sleeping site. The age and sex of these animals could not be determined but since FB was nulliparous when caught, it's unlikely that one of the other lorises was an infant. A non-collared,

and young-looking individual was observed on several occasions within 20 metres of FB and MD soon after the latter started moving off from their sleeping sites. It is thus very likely that this animal was part of the sleeping group. The fourth individual was only ever seen once at the sleeping site but never encountered throughout the night. The other group consisting of more than two individuals was that of FM, ML and a third individual. They were seen early on in the night before sunset, huddled together. As soon as night fell, one of them started moving away but remained within five metres. The sex and age of the third animal could not be determined.

Of all sleeping locations recorded for each individual, about two thirds consisted of a new location. Animals rarely used the same sleeping site two days in a row, preferring to change sleeping sites on a daily basis. Thus, they used the same sleeping site as the night before on average twice only (Mean = 1.9 $\pm$ 2.2) and moved an average of 72.4 m $\pm$ 67.8 between sleeping site locations. This distance differed substantially between animals (Table 3.15). The solitary and unsettled subadult female FG had the highest average distance between sleeping sites of all radio-collared individuals.

Table 3.15. Number of sleeping sites recorded for each animal, and of those, the different number of sleeping areas used. The mean distance (± SD) between sleeping site locations is given as an indication of how dispersed and 'unsettled' the animal is.

ID	Sex	Sleeping site fixes	Different sleeping sites	Mean distance between sites
FF	Female	9	5	35.8 ± 9.1
FE	Female	49	30	29.7 ± 2.8
FB	Female	45	32	38.4 ± 4.6
FI	Female	56	46	103.7 ± 11.4
FG	Female	18	17	300.0 ± 73.4
FK	Female	14	14	116.8 ± 17.0
FM	Female	6	6	83.8 ± 19.2
MJ	Male	18	15	78.9 ± 20.3
MA	Male	8	7	38.2 ± 5.6
MD	Male	45	30	37.9 ± 3.8
Ma	Male	3	3	20.7 ± 8.5
MT	Male	47	37	89.4 ± 12.5
MC	Male	3	3	14.9 ± 3.50
MH	Male	19	17	50.80 ± 11.7
MO	Male	10	8	70.9 ± 13.9
ML	Male	6	3	48.5 ± 29.9

Cohesiveness between sleeping partners

Radio-collared animals that formed groups did not always sleep together at the same sleeping site. To calculate the degree of cohesiveness at the sleeping sites, I measured Jacob's Index of association for each sleeping 'pair' (Table 3.16), with 0 indicating that animals never slept at the same site at the same time, and one indicating that animals always slept at the same sites together, pairs FK and MT and FB and MD, slept together more often than did other pairs. Female FE had two partners at different times. When she was first radio-tracked she was with partner MC but only three sleeping site locations were obtained for this male before he disappeared, all of which

coincided with FE's sleeping site locations. Following his disappearance male MH took over the area and slept with FE. He did not always share her sleeping site on a regular basis, instead sleeping within 20 metres or so and at times in a completely different area.

Table 3.16. Dynamic interactions between sleeping partners using sleeping site locations only. Positive values of Jacob's index (ranging from -1 to +1), indicate that animals were sleeping together. A value of +1 would indicate that animals always slept together whilst a value of -1 would indicate that individuals' simultaneous sleeping site locations are farther away from each other than by chance alone.

Sleeping partners	**Jacob's Index of cohesiveness**
FM and ML	0.7
FB and MD	0.9
FK and MT	0.9
FE and MH	0.6

3.5.7. Vocalisations

3.5.7.1. Calling frequency of different call types

Based on a total of 1720 calls described qualitatively in the field, five call types were heard and make up the following frequencies: the whistle (97.7 %), the chitter (2.0%), the mono-syllabic chitter (0.2 %), the 'krik' (0.05 %) and the 'zic' calls (0.05 %). The whistle ranged in the number of successive tones (units) that made up the call (phrase), from one tone to eight tones. The tones could either be 'long' or short, which sounded like 'peeps'. A whistle call could be made up of both long and short tones. Whistles with more than one tone, never consisted of just 'peeps'. The number of tones per call varied in the following proportions: one-tone (26.9 %), two-tones (49.2

%), three-tones (15.4 %), four-tones (4.2 %), five-tones (1.4 %), six-tones (0.3 %), seven-tones (0.24 %) and eight-tones (0.24 %) (Figure 3.23).

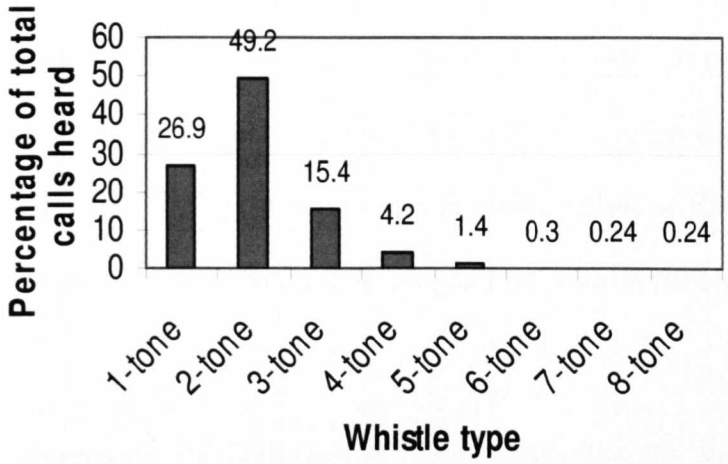


Figure 3.23. Percentage of whistles with different tone numbers based on a sample of 1680 whistles.

With regards to length of tone, the number of calls made up of only long tones accounted for the majority of whistles heard (92.2 %), whilst calls consisting of long tones as well as 'peeps' accounted for 7.8 % of all whistles. Calls with only a 'peep', were heard 11 times, making up less than one per cent of all calls heard. Preliminary examination of sonograms of one-tone and two-tone calls revealed a variety of call types based on visual characteristics of call structure and pattern. One-tone calls had nine different types, and two-tone calls had eleven types (see Davies 2006 for specific results). Further analysis of acoustic parameters would be required to qualify these whistle type variants as being distinct calls.

Apart from the whistle, which could be heard as far as 50 metres away, all other calls could only be heard within 10 metres of the animal and it proved impossible to make tape recordings.

3.5.7.2. Calling frequency of the whistle call

During the entire study period (20 months between 2004 and 2006), whistle calls (N = 1720) were uttered at an average of 0.8 $\pm$ 1.2 calls per hour (Median = 0.8) with a maximum of 30 calls in one hour and 85 in a six-hour night. Of the total 1720 calls heard during that period (2004 to 2006), 1064 calls were heard whilst radio-tracking focal animals (between August 2005 and July 2006). Of those 1064 calls, the identity of the caller (and thus its sex) could be assigned with 100% certainty to only 268 calls.

Based on this data set, 163 calls over 91 nights (range: 0 – 38), were uttered by females and 107 calls over 87 nights (range: 0 – 13), were uttered by males. No significant difference in hourly calling rate was found though between males (Median = 0.3) and females (Median = 0.2) (MWU = 17.0, $n_1 = 7$, $n_2 = 7$, ns) (Figure 3.24). When the sex of the caller could not be ascertained I recorded whether the call was made in the vicinity of a female or a male (usually a radio-collared individual). Thus, over 91 nights, 606 calls were uttered in the presence of a female (range: 0 – 61) and over 87 nights, 470 calls (range: 0 – 45) were uttered in the presence of a male. No significant difference was found in hourly calling rate between males (Median = 0.6) and females (Median = 0.9) (MWU = 15.0, $n_1 = 7$, $n_2 = 7$, ns) (Figure 3.24).

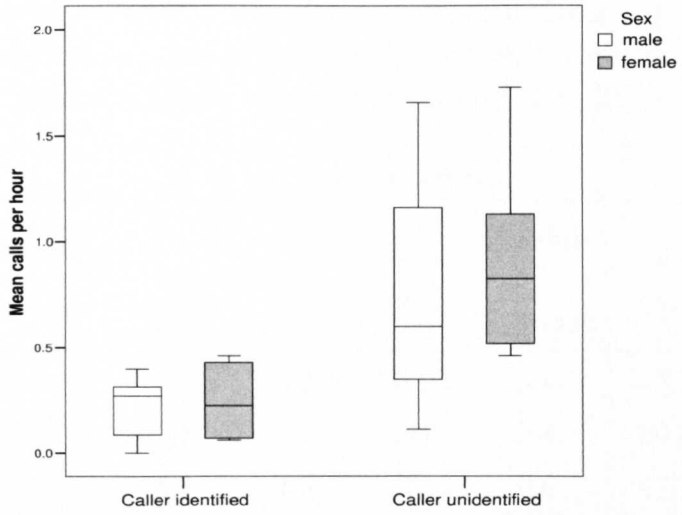


Figure 3.24. Mean number of calls per hour uttered by males (N = 7) and females (N = 7). Two conditions are presented: one where the sex of the caller could be identified (caller identified) and one where the sex of the caller could not be identified but the call was uttered in the vicinity of a loris whose sex was known (caller unidentified). The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

3.5.7.3. Contextual use of calls

Whistles were heard in a variety of contexts. The context in which different whistle types were uttered could only be determined for 55.5 % of the total number of calls heard during the tracking period (N = 1064). Of those, 32.3 % were between known paired animals, 27.7 % occurred prior to or during travelling, and were not returned by other loris calls, 27.2 % were between animals whose identities were unknown or between a radio-collared animal and at least one other animal whose identity was unknown, 6.1 % were between an unpaired male and female, 2.7 % between females, 3.2 % between mother and infant and 0.7 % in the presence of a predator. Some call types were uttered more frequently within a specific context (Table 3.17).

Table 3.17. Frequency at which each call type was heard across different contextual categories. The whistles are classed according to number of tones making up the call (1t, 2t, 3t, or > 4t) and whether the call included 'peeps' (1tp, 2tp).

	Context						
Call type (N)	Unidentified Animals	♀-♂ non-pair	♀-♀ or ♂-♂	♀-♂ pair	Adult - young	Spacing/ Travelling	Predator presence
1t (147)	23.8	5.4	8.2	42.2	3.4	15.7	1.4
2t (255)	34.9	3.5	1.2	36.5	2.4	20.8	0.8
3t (86)	20.9	8.1	1.2	22.1	0.0	47.7	0.0
> 4t (27)	5.0	31.4	0.0	6.4	0.0	57.3	0.0
1tp (11)	54.6	0.0	0.0	18.2	27.3	0.0	0.0
2tp (14)	21.4	14.3	0.0	35.7	0.0	28.6	0.0
3tp (10)	30.0	0.0	0.0	10.0	30.0	30.0	0.0
> 4tp (25)	0.0	0.0	0.0	5.8	2.5	91.7	0.0
Chitter (12)	23.3	55.0	0.0	16.7	5.0	0.0	0.0
Zic (1)	0.0	0.0	0.0	0.0	100.0	0.0	0.0
Krik (1)	0.0	0.0	0.0	100.0	0.0	0.0	0.0

Male-female interactions:

Calls between males and females occurred in two contexts: calls between males and females that did not form part of a sleeping group, and calls between sleeping group 'pairs'. The first case was observed between one male and one female whose home ranges were exclusive. They engaged on three non-consecutive nights in a form of a vocal 'battle' whilst pacing up and down the edge of the female's home range. The male attempted to venture into the female's home range on several occasions, whilst the female stayed on the border of her home range. Approximately 80 % of eight-tone calls and 50 % of chitter calls heard during the study were uttered in this context.

Individuals that formed a 'pair' often engaged in whistle counter-calling and would result in animals leaving the sleeping site and going their separate ways, or animals meeting during the night or at dawn. In both cases one- and two-tone calls were the most frequently used, followed by three-tone calls. Calls with more tones were never heard in this context.

Territoriality, spacing:

Calls did not always occur in the presence of another loris or as part of a vocal exchange. Lorises often whistled without a reply (29.2 % of all calls heard). An extreme example of such behaviour was observed on the 14th of February 2006 whilst tracking female FI. She would utter a call and subsequently move off, doing so repeatedly around the perimeter of her home range. All calls contained more than five tones, including peeps. All whistles with more than five tones heard during the entire study period were uttered by this female during that night. A total of sixty one calls were uttered and less than six were answered. She eventually settled and carried on without calling for the rest of the night. Her average calling rate at other times was of 0.04 calls per hour. She was also seen trail marking and one other loris was known to be present in the area at the time but did not engage in a vocal exchange.

Group dynamics:

Average hourly calling rate was highest between 19.00 and 20.00 when animals dispersed from their sleeping sites (Figure 3.25) and were usually uttered between members of a sleeping group and neighbouring animals whose sleeping sites were within 30 metres. Similarly, a peak in calling rate occurred between 05.00 and 06.00 when animals start moving back towards their sleeping sites to join members of their sleeping group (see section 3.3.1. for activity rhythms). Unlike the louder whistles

uttered during group dispersal, these calls were uttered between members of a sleeping group, at close proximity and included short, quiet tones. Average calling rate remained relatively high throughout the night.

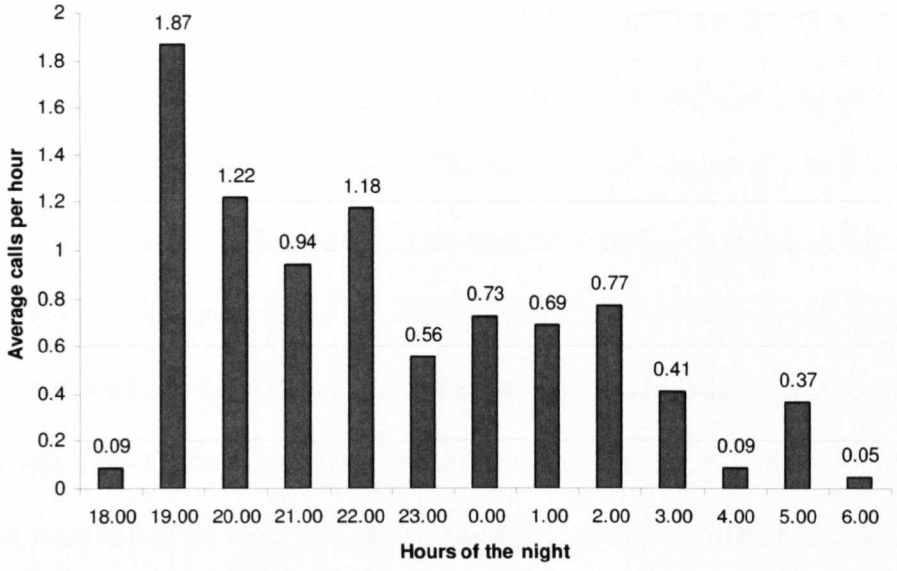


Figure 3.25. Average number of whistle calls uttered per hour for each hour of the night (N = 1720).

Mating and advertising:

The night of highest calling frequency occurred during a three-day period in late February 2005. Whistles of between one and four tones were exchanged between four and six animals at a rate of up to 30 calls per hour, with the majority occurring between approximately 19.30 and 22.00. Up to six animals were observed chasing each other, grooming, or simply calling and moving frantically within a small area (< 30 m^2). The first night, 28 calls were heard between 11.00 and 06.00. The second night a total of 45 calls was uttered in the first three hours of the night, with the first call uttered at around 19.36. In the third night, 85 calls were uttered again in the first three hours of the night, starting at 19.22. The fourth night, 48 calls were uttered

between 19.23 and 21.38. The next night, only two lorises were seen and one call uttered at 19.51.

Adult-infant interactions:

The chitter call was heard during rough play between an adult (either the mother or in some cases unidentified sex) and a juvenile. Whistles were the most frequently heard call type between a mother and an infant. The majority of 'one peep' calls were uttered between a mother and an infant. Sonographic display of whistles uttered in the context of mother and infant (N = 32) revealed seven cases of two overlapping whistles heard exclusively in the context of a mother parking its infant or picking it up (Figure 3.26). These calls were heard whilst observing the one month old infant and all synchronous calls that were recorded in the field (as one call) appear to have come from the mother.

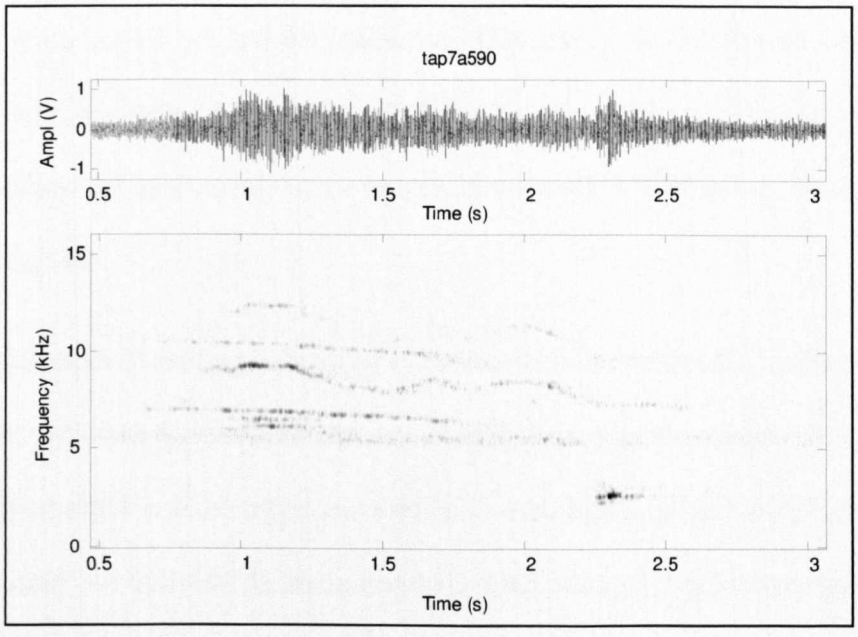


Figure 3.26. Sonographic display of synchronous calls uttered by a mother (long, undulating one-tone whistle) and its infant (short, straight one-tone whistle showing below mother's whistle).

3.5.8. Mating behaviour and breeding seasonality

3.5.8.1. Qualitative description of mating behaviour

Although no act of mating was ever observed, behaviours associated with mating were recorded during three separate events, one in March, one in November and one in September. Such behaviours involved a general increase of activity and more than the usual number of lorises present within a small area. On each occasion that a potential mating event was observed, as few as two males and as many as five males were observed chasing each other away and chasing after a female presumed to be in oestrous. In two cases such behaviour was accompanied by a high frequency of whistles between the males and chitter calls from the female. The exception occurred during the event in September when one of the radio-collared males MA was observed chasing a female with another male following behind for approximately 20 minutes. No whistles were heard between the males. Instead the female uttered several chitter calls, some of which lasted continuously over one minute. Eventually the other male moved off and the female and MA stayed around the same area for about 15 minutes before MA moved off. Whether this series of events constituted the chasing behaviour associated with a female in oestrous is difficult to interpret without further evidence.

Another example of mating behaviour occurred between male MD and female FB, who at the time was not collared but was caught soon after this event. This event occurred one night in November. Several calls were heard in MD's area and appeared to be between 3-4 individuals, including MD. One young animal who shared MD's home range was not taking part in this event and just rested nearby without paying much attention. Behavioural observations of the animals were difficult as most

interactions occurred high up in the canopy and visibility was poor. Much of the activity took place early in the evening (between 19:00 and 21:00) and consisted of some chases and a high frequency of whistle calls and chitter calls. Following that night, things appeared to get back to normal and MD was seen sharing his sleeping site with the young female FB and a third loris. After that night MD spent a lot more time around the sleeping site area, and within 30 metres of FB, which was different to the ranging behaviour he had exhibited previously whereby he would interact with the two lorises for a short period of time at the sleeping site then move off to another part of his home range. This 'protective' ranging behaviour lasted a week after which he resumed his normal ranging patterns. The female FB was caught early December and found to be pregnant.

The third event associated with mating occurred before the radio-tracking study started, in an area with high slender loris density. Unlike the events described previously this one occurred over a period of four days, early March. It involved several males (four to five) chasing one female from approximately 19.00 to 22.00. Animals uttered several whistle calls resulting in the highest calling frequency recorded (see Section 3.5.6). This was repeated the three following days but with less males present each night. The fourth night only one male and one female remained.

3.5.8.2. Breeding seasonality

To identify whether breeding seasons occurred in MPFR I estimated seasonality of births by plotting the approximate age of infants/juveniles caught, on the growth curve of *Loris tardigradus* by Rasmussen and Izard (1988). There appears to have been two births in April (Male Juvenile 1 (MJ1) and Juvenile 4 (J4)), one between mid August

and early September and one in October. Assuming that gestation length is approximately 165 days (Rasmussen and Izard, 1988), this would suggest conception periods around November and one between March and May.

I also compared average monthly home range size and nightly path length throughout the year (Figures 3.27 and 3.28). An increase in home range size and path length may be interpreted as a male venturing outside his normal home range and travelling further distances to mate with a neighbouring female, whilst an increase in home range size and mean path length may be interpreted as a female advertising her status to neighbouring males by encroaching into their home range and travelling along the border of her home range to advertise her status. The female in this case might be interested in enhancing the genotypic diversity of her offspring or gaining access to the superior quality of extra-pair males (Fietz, 2003). In addition, female lorises have been observed to increase their home range size during potential breeding seasons (Kar Gupta, 2007; Radakrishna and Singh, 2002). A similar monthly pattern in home range size and mean path length may indicate breeding seasonality.

Since the reproductive status of most females being radio-tracked could not be ascertained with regards to whether or not they were reproductively active during the time of tracking (except for two females who were in oestrous when caught and one female who was pregnant when caught and subsequently gave birth), graphic representations of home range size and nightly path length variation throughout the year are presented for each sex separately to avoid any diluting effect on potential changes in ranging behaviour as a direct effect of reproductive seasonality (Figures 3.27 and 3.28). The patterns presented in figure 3.28 thus must be interpreted with

care since some females may not have been reproductively active during the time they were tracked and their ranging patterns would not have changed as a result.

Figures 3.27 and 3.28 demonstrate that monthly plots of mean nightly path length follow a similar pattern to mean home range size, for both males and females although sample size was too small to allow statistics to be used. In both males and females, nightly path length and home range size increased in March and April, whilst in males, home range size and mean path length also increased in November. [1]

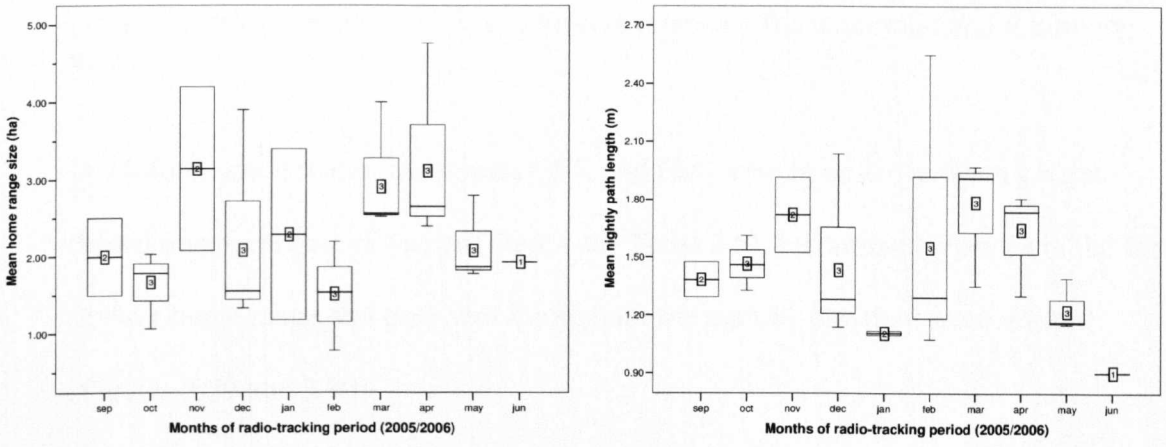


Figure 3.27. Variation in home range size (left) and nightly path length (right) between August 2005 and June 2006 for males (N = 8; note the number of animal differs for each month. Data were available only for one male in June (last of four months for male MH) whilst two males (MD and MT) were tracked for a period of six months, one from September and one from November). The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

[1] Care should be taken in interpreting these results as an uneven number of individuals were tracked in each month of the year. This is particularly relevant for females whereby some females may not have been reproductively active in that particular year.

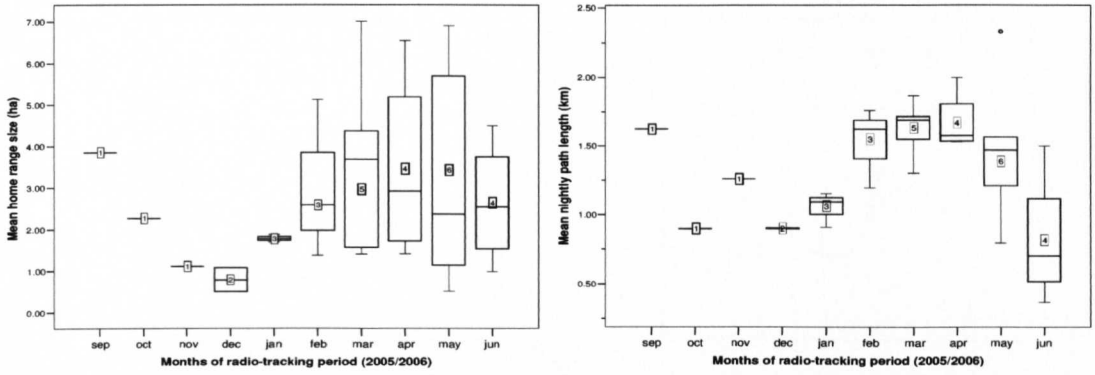
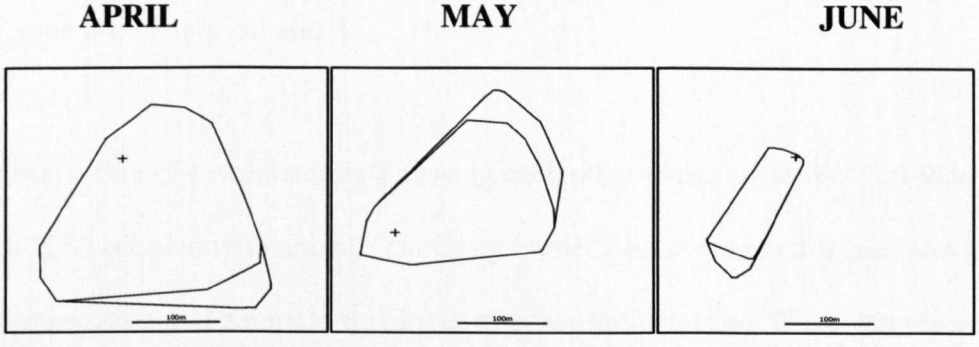


Figure 3.28. Variation in home range size (left) and nightly path length (right) between August 2005 and June 2006 for females (N = 7; note the number of animal differs for each month. Only one female (FF) was tracked during the months of September, October and November whilst two females (FE and FB) were tracked for a period of six months from December). The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

In addition, since two of the females, FK and FM, were in oestrous when caught (based on appearance of vaginal cleft – see Table 3.5), I examined changes in the size of their home range and core area throughout the months that they were tracked (Figures 3.29 and 3.30).



5.7 ha - 5.1 ha (33 fixes) 3.8 ha - 3.3 ha (35 fixes) 1.0 ha - 0.8 ha (26 fixes)

Figure 3.29. Changes in monthly home range size for female FM caught on 06.04.2006. Maximum home range is depicted in black (calculated using MCP 100%) and core area in blue (calculated using MCP 85%). Home range sizes and core area sizes are given along with the number of location fixes used to calculate them. This female was in oestrous when caught and was paired with male ML.

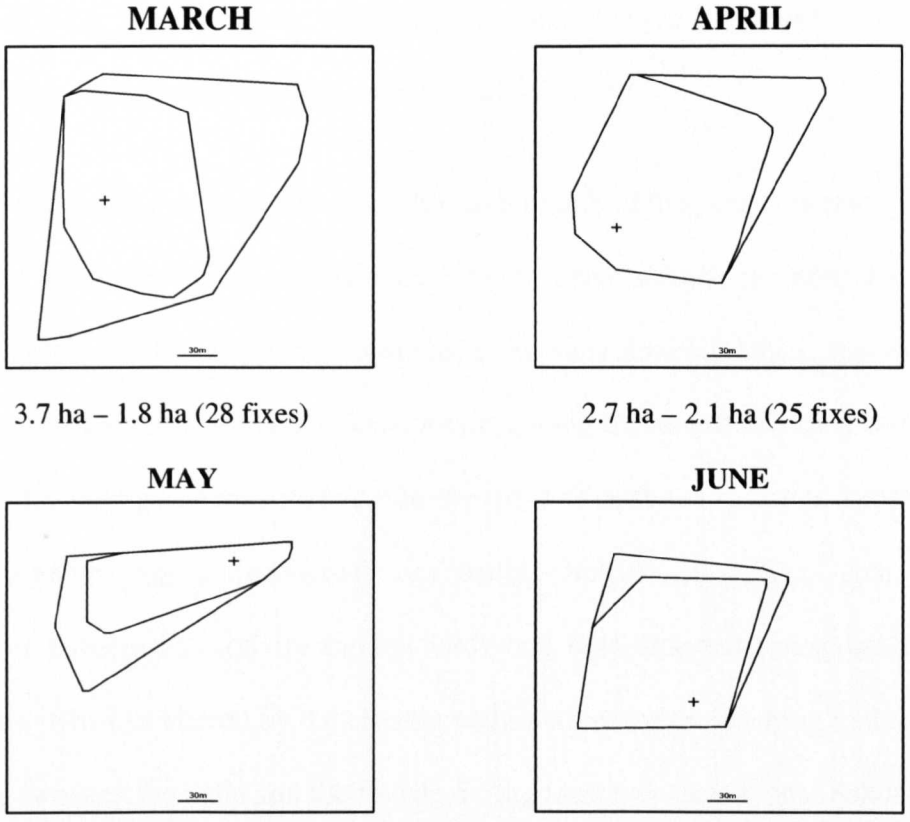


Figure 3.30. Changes in monthly home range size for female FK caught on 04.03.2006. Maximum home range is depicted in black (calculated using MCP 100%) and core area in blue (calculated using MCP 85%). Home range sizes and core area sizes are given along with the number of location fixes used to calculate them. This female was in oestrous when caught and settled with male MT soon after being caught.

The observation of several animals chasing each other over a three day period in early March 2005 coupled with animals calling at higher than average rates (see previous section) suggests that a female was in oestrous during that time. The event observed between MD and FB in November, coupled with the fact that FB gave birth around April, suggests that she was in oestrous in November. Finally, the female who was observed pacing her home range in late February 2006 whilst uttering several calls

and trail marking may have been advertising her reproductive status and home range boundaries, in order to attract neighbouring males.

Finally, I compared average calling rate for each month of the year between September 2004 and August 2006 (Figure 3.31) by using all calls recorded during that year (N = 1064) (calls that could be assigned to an individual (and thus, sex) were limited and would have resulted in some months being represented by only one sex). I assumed that calling rate may increase during times of oestrous as males compete for the female and engage in intra-sexual vocal battles (Nekaris, 2000; Kar Gupta, 2007). In addition, females (in captivity and the wild) have been reported to respond to the 'appeasing' whistles uttered by the chasing male with whistles, resulting in duets occurring between the male and the female during such pair formations (Schulze and Meier, 1995; Kar Gupta, 2007). In this study, both males and females appeared to be calling during mating events and no significant inter-sexual difference in hourly calling rate was found. Figure 3.31 shows that calling rate was at its highest during the month of November, but were relatively low during the months of March to May.[2]

[2] Care should be taken when interpreting these results as calls also were uttered in contexts other than mating and within the context of mating, not all females would have been reproductively active during that year.

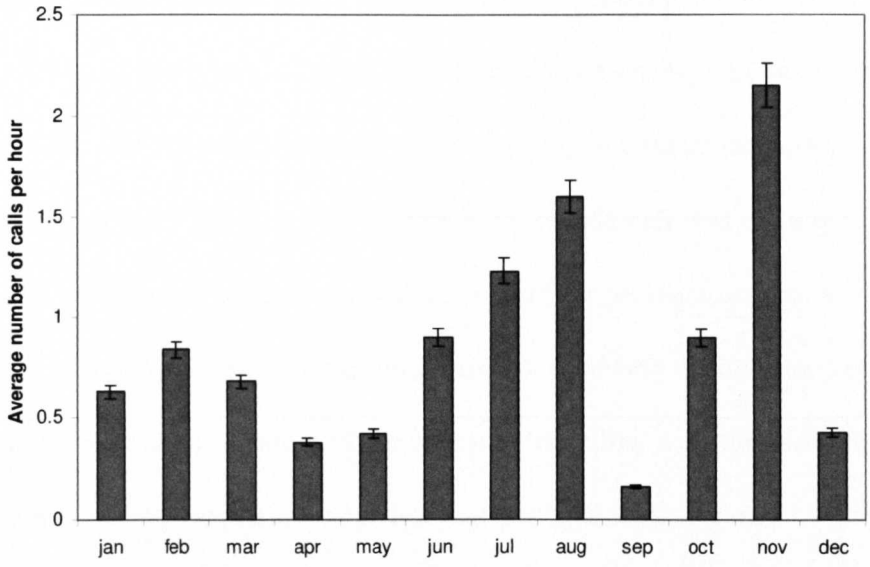


Figure 3.31. Average (± SD) calling rate (number of whistle calls per hour) for each month of the year.

Summary

- Lorises at MPFR were social on average 21.4 % of the time and 18.0% of the time (within 30 metres and 20 metres of other individuals, respectively). Lorises were mostly social with just one other loris but were also observed in the presence of two and three lorises. Lorises were more social (> 50%) at the sleeping site (early and late hours of the night) but nevertheless remained social throughout all hours of the night (> 10%). Neutral interactions were the most frequently recorded followed by positive indirect interactions. Negative and direct interactions such as fighting were rare. Members of a spatial pair associated significantly more frequently than non-spatial pairs and positive interactions only occurred between members of a spatial pair.
- Lorises that formed pairs showed on average high degrees of cohesiveness, which varied between pairs. The majority of sleeping groups consisted of two

individuals, usually a male and a female but in two cases groups consisted of three or four animals. Members of a pair also showed high levels of cohesiveness at the sleeping site. Lorises rarely used the same sleeping site on consecutive nights.

- Five call types were heard at MPFR. The loud whistle call was the most frequently heard and was uttered in various contexts, including communication between members of a pair, unpaired males and females, members of the same sex and adults and their young, context of spacing and travelling and predator presence. The highest calling frequency recorded was during a mating event.
- Based on the observations of mating behaviour and the results from estimated times of birth, monthly home range size patterns, mean nightly path length and monthly calling rate patterns, there appears to be two potential conception periods: one in November and a longer one between the months of March and May. Females showed some trend for home range enlargement during times of oestrous.

3.6. HABITAT AND MICROHABITAT USE

3.6.1. Slender loris density across different areas within MPFR

Based on the number of caught animals and associated conspecifics, a density estimate was obtained for each of three areas which had been surveyed to describe their vegetation characteristics. Area NL (No Loris area), was the smallest of the three (11.5 hectares) and found between survey path (VP3) and an extensive matrix of paddy fields (Figure 2.5), and had the lowest density with 0.2/ha. Area SS2 (12.5 hectares), was situated between survey paths VP1, VP2 and VP3 and had the highest density at 0.9/ha. Area SS1 (36 hectares), with actively managed pine forests on either

side, had a density of 0.3/ha. Table 3.18 below describes the vegetation characteristics of each of these three areas (see Section 2.4 for methodology).

Table 3.18. Vegetation characteristics of areas NL (No Loris area with a slender loris density of 0.2/ha), SS1 (Study Site area 1 with slender loris density of 0.3/ha) and SS2 (Study Site area 2, with the highest slender loris density of 0.9/ha). Values for the average number of trees, species and families are calculated per 10 m x 10 m plot (0.01 ha).

	Surveyed Sites (loris density)		
Stand characteristics	NL (0.2/ha)	SS1 (0.3/ha)	SS2 (0.9/ha)
Disturbance level	Undisturbed	Disturbed	Disturbed
Predominant vegetation	Trees	Trees and shrub	Small trees
Maximum height of vegetation	20-30 m	20-30 m	5-10 m
Density of undergrowth	Low	High	Medium
Cover/abundance of *O. stridula*	3	4	1
No of trees with cbh $\geq$ 10 cm	163	177	187
Relative % of *H. laurifolia* trees / 0.01 ha	36.3	32.2	54.3
No of species	28	42	34
No of families	18	16	13
Mean no. of trees / 0.01 ha	20.4 $\pm$ 6.5	18.5 $\pm$ 4.2	18.7 $\pm$ 5.5
Mean no. of species / 0.01 ha	9.5	9.0	7.4
Mean no. of families / 0.01 ha	2.2	1.7	1.3
Tree species with highest IVI	*Dipterocarpus zeylanicus*	*Humboldtia laurifolia*	*Humboldtia laurifolia*
Shannon-Weiner index	1.9	2.0	1.5
Simpson's Index	0.2	0.2	0.3
Average tree basal area per plot (m^2/ha)	2.4 $\pm$ 1.5	3.8 $\pm$ 2.9	2.2 $\pm$ 0.8

The tree species *Humboldtia laurifolia* was dominant in survey sites 1 and 2 (SS1 and SS2), whilst *Dipterocarpus zeylanicus* was the most dominant species in NL. In

addition, the bamboo species *Ochlandra stridula* was extensive in areas NL and SS1 but seldom found in area SS2 (Table 3.18). In fact, areas with a high cover of *O. stridula* had little *H. laurifolia* and vice versa. Area NL had the highest average number of families and average number of species per plot but area SS1 had the highest Shannon-Weiner's index of species diversity (H = 2.0). Area SS2 had the lowest average number of species and families and the lowest Shannon-Weiner diversity index (H = 1.5). The concentration of dominance (Cd), expressed as Simpson's index, was quite low for SS1 (Cd = 0.2) and highest for SS2 (Cd = 0.3). Basal area was highest for SS1 at an average tree basal area of 3.8 and lowest for SS2 at an average of 2.2 m^2/ha (Table 3.18). Calculation of Sorensen's Index of Similarity between sites revealed that area NL shared 51% of its species with site SS1 and 37% with site SS2, whilst site SS1 shared 46% of its species with site SS2.

Lorises at MPFR were not found in anthropogenically disturbed areas (actively managed plantations, home gardens), but they did use regenerating pine forests and patch perimeter habitat pine forest edges, forest edge along home gardens and paddy field edges (see Figure 3.8). These areas were mainly frequented during foraging activities. Disturbed areas were typically characterised by large canopy gaps, due to the small density of large mature trees, a high density of lianas and vines and shrubs and a relatively low level of species diversity. This was particularly so for the area with the highest slender loris density (SS2: Shannon-Weiner Index = 1.5). This area was dominated by *H. laurifolia*, which resulted in the concentration of dominance being the highest in this area in comparison to other areas within MPFR.

3.6.2. Habitat types within home ranges

Lorises at MPFR never observed using actively managed plantations, agricultural fields or home gardens (Table 3.19). They did use regenerated pine plantations and the edges of regenerating paddy fields where bushes and undergrowth had taken over.

Table 3.19. Microhabitat characteristics of four habitat types found within the study area: agricultural land (paddy fields, banana, cinnamon), forest plantations (pine forest, rubber), regenerated plantations (pine only), home gardens and forest. Mean plant height was not calculated for forest plantations. Instead, the range of height of trees (pine and rubber for plantations and pine only for regenerated plantations) and shrubs (in regenerated plantations) is given.

	HABITAT TYPES				
Microhabitat features	Agricultural land (~20 ha)	Forest plantations (~ 50 ha)	Regenerated plantations (~1 ha)	Home gardens	Forest (~ 64 ha)
Slender loris presence/ Absence	Absent except edge	Absent except edge	Present	Absent	Present
Connectivity (%)	None	None	0-25	26-50	0-25
Lianas	None	None	None	None	Occasional
Mean plant height (m) or height range	N/A	15 – 20	Trees: 15 - 20 Shrubs: 1 - 2	17.2 $\pm$ 2.9	12.3 $\pm$ 5.5
Most common plant species	*Lantana* spp. and *O. stridula*	*Pinus* spp.	*Pinus* spp. *Hedyotis fruticosa* *Clerodendrum infortunatum* *Alstonia macrophylla*	*Alstonia scholaris* *Mangifera indica* *Artocarpus heterophyllus* *Areca catechu* *Cocos nucifera*	See Appendix 7

I calculated the amount of interior forest, patch perimeter habitat and regenerating habitat within each loris' home range (Table 3.20). For some animals, their home

range was situated away from plantations, home gardens or agricultural plantations and thus 100% of their home range consisted of forest interior habitat.

Table 3.20. Percentage of different habitat types (interior forest habitat, patch perimeter habitat and regenerating habitat) available and used, within the home ranges of 14 lorises (7 males and 7 females). The home ranges of two of those lorises (male MC and female FF) consisted solely of interior forest habitat.

	Interior forest habitat		**Patch perimeter habitat**		**Regenerating habitat**	
	% Available	% Used	% Available	% Used	% Available	% Used
MJ	57.5	64.6	29.6	35.4	12.9	0
MA	73.4	90.7	5.6	9.3	21	0
MT	86.5	97	4.5	1.2	9	1.7
MO	97	86.4	3	13.6	0	0
MH	86.6	66.1	5	33.9	8.4	0
MC	100	0	0	0	0	0
MD	94.1	84.1	4.7	15.9	1.2	0
FK	87.6	97.6	6.2	1	6.2	1.4
FI	93.5	85	4.5	15	2	0
FB	92.8	87	6.1	12.8	1.1	0.1
FG	93.3	56	3.6	18.5	3.2	25.5
FM	90.4	59.1	8.5	10.8	1.1	30.1
FE	89.3	87.1	9.1	12.9	1.6	0
FF	100	0	0	0	0	0

Of the three types of habitat measured within loris home ranges (for those 12 lorises who had all three habitat types within their home range) patch perimeter habitat was the only one to show a significant difference between percentage availability and

percentage use, with lorises using this habitat type significantly more than was available within their home ranges (Wilcoxon matched-pairs signed ranks test: z = -2.5, p = 0.009). No significant difference between percentage availability and percentage use was found in interior forest habitat (z = 1.1, n.s.) and regenerating habitat (z = -1.1, n.s.) (Figure 3.32).

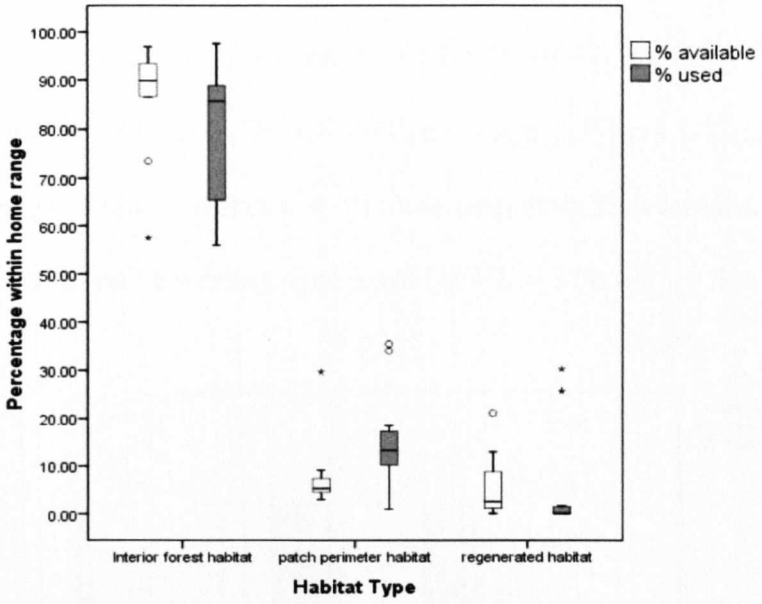


Figure 3.32. Percentage of three different habitat types, interior forest habitat, patch perimeter habitat and regenerating habitat, within the home ranges of 12 lorises. The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

3.6.3. Microhabitat use

3.6.3.1. Plant species

A total of 49 plant species were recorded during vegetation surveys and their IVI calculated. Of those 49 species, lorises (N = 17) used the eight most dominant species (*H. laurifolia, O.stridula, D. retusa, A. nobilis, M. zeylanicus, S. walkeri, D. zeylanicus* and *S. macrophylla*) on average 58.6 % (± 43.4) of the time. Of those eight

species, *H. laurifolia*, *O. stridula* and *D. retusa* accounted for 45.2 % (± 41.3) of total observations. *Swietenia macrophylla*, was the least used dominant species (Mean = 1.6 % ± 5.3).

Although females appear to use *H. laurifolia* (Median = 50.0) and *O. stridula* (Median = 12.5) more frequently than males (Median = 20.0 and 10.0, respectively), no significant inter-sexual difference was found (*H. laurifolia*: MWU = 172.0, $n_1 = 8$, $n_2 = 9$, ns; *O. stridula*: MWU = 179.5, $n_1 = 8$, $n_2 = 9$, ns) (Figure 3.33). Similarly, males appear to use *D. retusa* (Median = 40.0) more frequently than females (Median = 11.0), but the difference was not significant (MWU = 174.5, $n_1 = 8$, $n_2 = 9$, ns).

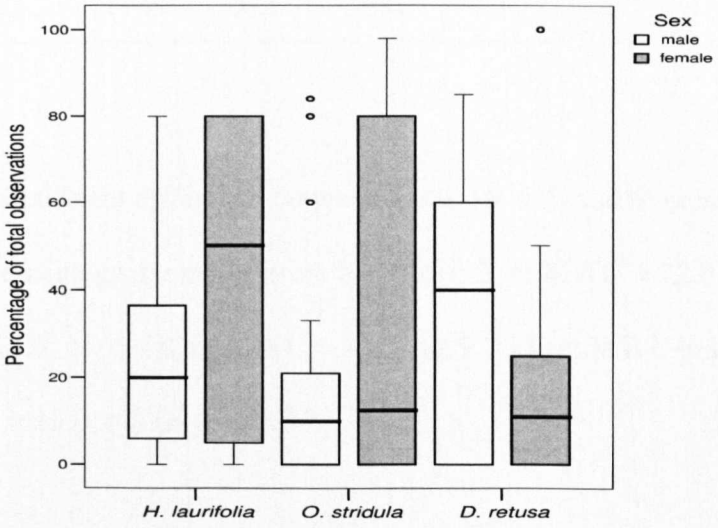


Figure 3.33. Percentage use by males (N = 9) and females (N = 8) of the three most frequently used dominant species (*H. laurifolia*, *O. stridula* and *D. retusa*). The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

3.6.3.2. Height

Lorises were most frequently observed using heights between three and five metres and between six and eight metres and seldom used heights above 12 metres (Table 3.21).

Table 3.21. Percentage use of different height classes by lorises (N = 17) in MPFR.

	Height classes				
Descriptives	**< 2**	**3 – 5**	**6 – 8**	**9 – 11**	**> 12**
Median	23.5	28.0	29.5	17.3	0.0
Minimum	0.0	4.8	0.0	0.0	0.0
Maximum	89.3	56.9	63.6	48.8	9.6
Interquartile range	26.2	11.7	26.5	36.0	3.2

There was no significant difference between males (N = 9) and females (N = 8) in average percentage use of different heights (< 2 m: MWU = 22.0, ns; 3 – 5 m: MWU = 15.0, ns; 6 – 8 m: MWU = 21.0, ns; 9 – 11 m: MWU = 16.0, ns; > 12 m: MWU = 15.0, ns) (Figure 3.34).

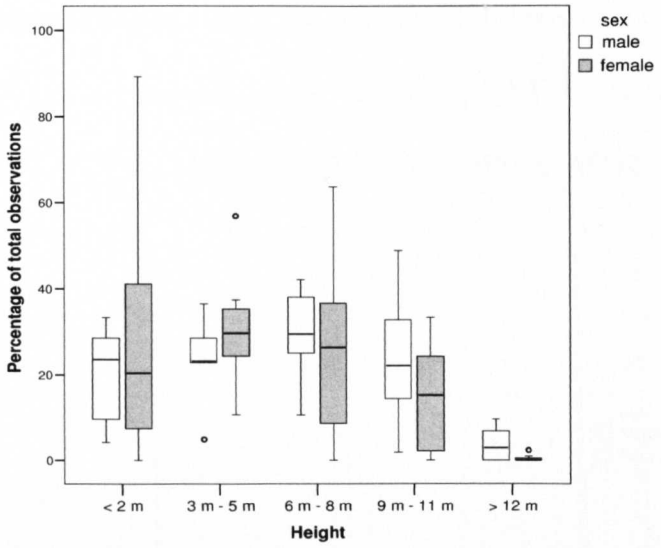


Figure 3.34. Percentage of total observations for which males (N = 9) and females (N = 8) were observed at various ranges of heights (m). The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

3.6.3.3. Connectivity

Lorises used areas of low connectivity most frequently, followed by areas of medium connectivity, high connectivity and very high connectivity (Table 3.22). Results from the 130 random points selected within the study site also report areas of low connectivity as being the most frequent (Median = 57%).

Table 3.22. Percentage use of different levels of connectivity (within a 5 m radius) by lorises (N = 17) in MPFR.

	Connectivity levels within a 5 m radius			
Descriptives	**0 – 25 %**	**26 – 50 %**	**51 – 75 %**	**75 – 100 %**
Median	68.6	18.3	16.7	1.3
Minimum	0.0	0.0	0.0	0.0
Maximum	100.0	50	50	5
Interquartile range	41.7	28.6	23.7	1.3

There was no difference in percentage use of areas of different connectivity levels between males (N = 9) and females (N = 8) (0 – 25 %: MWU = 12.0, ns; 26 – 50 %: MWU = 16.5, ns; 51 – 75 %: MWU = 11.5, ns; 76 – 100 %: MWU = 20.0, ns) (Figure 3.35).

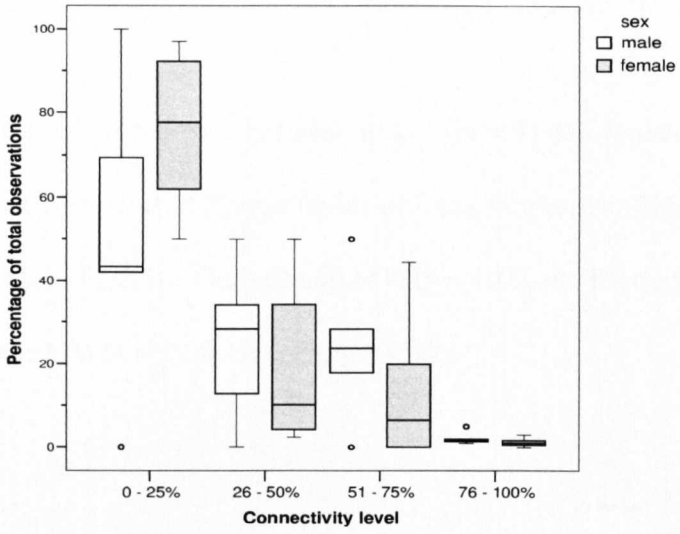


Figure 3.35. Percentage use by males (N = 9) and females (N = 8) of areas with different connectivity levels. The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values. upper (75%) quartiles, respectively.

Overall, lorises mostly used areas where presence of lianas was recorded as being abundant (five or more lianas) and frequent (four to five lianas). They used areas where liana presence was recorded as occasional (two to three lianas) slightly less frequently and areas where lianas were rare or absent least frequently (Table 3.23).

Table 3.23. Percentage use of different levels of liana frequency by lorises (N = 17) in MPFR.

	Levels of liana frequency within a 5 m radius			
Descriptives	**Rare**	**Occasional**	**Frequent**	**Abundant**
Median	3.1	14.6	16.7	40.7
Minimum	0.0	0.0	0.0	0.0
Maximum	36.0	100.0	72.7	100.0
Interquartile range	23.9	35.0	33.8	45.7

There was no significant difference between males (N = 9) and females (N = 8) in frequency of use of areas with different levels of liana frequency (Figure 3.36) (Absent/rare: MWU = 12.0, ns; Occasional: MWU = 10.0, ns; Frequent: MWU = 13.0, ns; Abundant: MWU = 12.0, ns) (Figure 3.36).

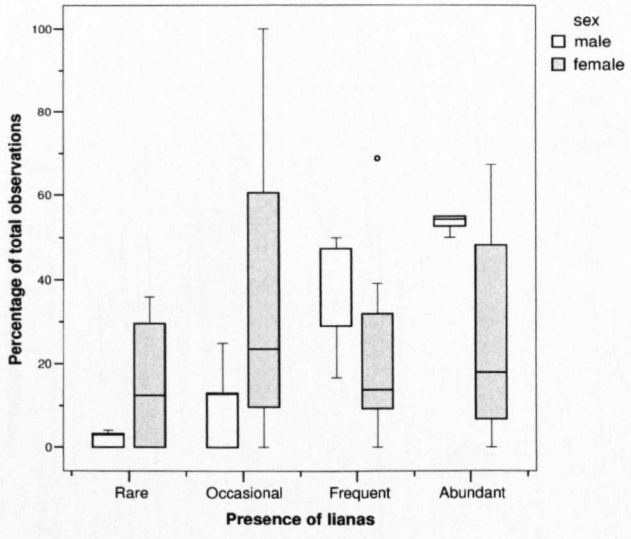


Figure 3.36. Percentage use by males (N = 9) and females (N = 8) of areas with different levels of liana frequency. The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

3.6.3.4. Substrate Use

Substrate type

Lorises (N = 17) used branches more frequently than other substrate types (Median = 36.0, IQ range = 15.3, Range = 20.0 – 60.0), followed by lianas (Median = 21.5, IQ range = 15, Range = 0.0 – 50.0).

Inter-sexual difference was near significant for frequency of use of branches (Males: median = 30%; females: median = 43%) (MWU = 8.0, n 1 = 9, n 2 = 8, z= -1.862, p = 0.06) and lianas (Males: median = 31%; females: median = 12.5%) (MWU = 8.0, n 1 = 9, n 2 = 8, z = -1.867, p = 0.06), with males using lianas more frequently and branches less frequently than females (Figure 3.37).

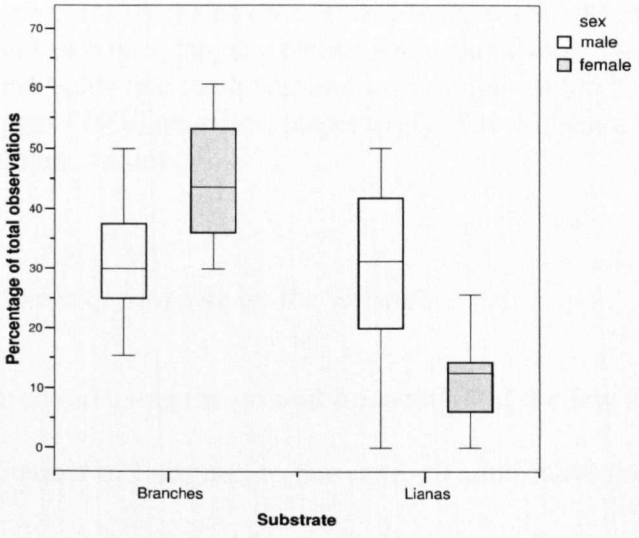


Figure 3.37. Percentage use by males (N =9) and females (N = 8) of the two most frequently used substrates: branches and lianas. The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

There were no differences between males (N = 9) and females (N = 8) in average percentage use of other substrate types (Terminal branches: MWU = 17.0, ns; Vines: MWU = 19.0, ns; Tangles: MWU = 19.5, ns; Trunks: MWU = 12.0, ns; Ground: 17.0, ns) (Figure 3.38).

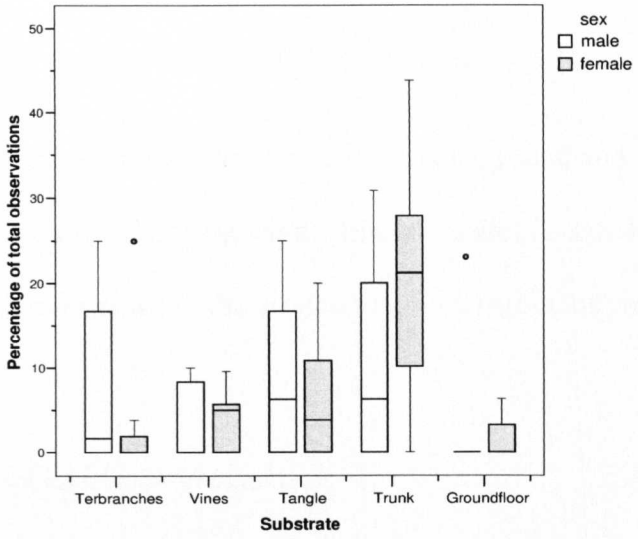


Figure 3.38. Percentage use by males (N = 9) and females (N = 8) of other substrate types: terminal branches, vines, tangles, trunks and groundfloor. The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

A qualitative description of foraging on the ground:

Lorises were not observed using the ground frequently but the few times they did it was always in the context of foraging. In one case, an adult radio-collared female, FE, was observed foraging on the ground for about 26 minutes. Before descending on the ground she would remain still for a few minutes and explore her surroundings. She would then rapidly climb down a liana or trunk descending all the way to the ground and remain on it for a few more minutes whilst exploring her surroundings a few more times, as well as looking down on the ground. Once she was comfortable with the safety of moving onto the ground she would slowly and awkwardly walk on the

ground, whilst always staying near a root or liana, which would give her access to a safe height. She would lift up leaves and look underneath. She would quickly pick insects up with one hand and explore her surroundings whilst chewing. If the insect was large she would grab it, put it in her mouth and quickly climb up to a safe height of at least one meter high to finish eating the insect. She would then repeat the same process. This entire foraging session lasted about 25 minutes.

Lorises would more often spot an insect moving on the ground and run down rapidly to catch it and run back up. Foraging would thus occur from a safe height and the animal would only climb down to the ground to grab a particular prey spotted near the base of the tree.

Other activities associated with ground use

On one occasion, a young female in oestrous was observed travelling on the ground, whilst two or three males were in the trees above chasing each other and trying to reach the female. She was trying to escape from the males and in doing so ended up going down on the ground and walking to a nearby sapling that was isolated and inaccessible to the males.

Substrate size

Lorises were observed using small substrates more frequently than other size classes, with large substrates being used the least frequently (Table 3.24).

Table 3.24. Percentage use of substrates of different size by lorises (N = 17) in MPFR.

	Substrate Size			
Descriptives	Very small	Small	Medium	Large
Median	22.1	55.1	23.0	3.9
Minimum	0.0	25.0	0.0	0.0
Maximum	43.5	71.1	75.0	12.5
Interquartile range	16.8	21.5	15.0	5.2

There was no inter-sexual difference in average percentage use of different substrate sizes between males (N = 9) and females (N = 8) (≤ 5 cm: MWU = 22.5, ns; 6 – 10 cm: MWU = 16.0, ns; 11 – 15 cm: MWU = 13.0, ns; > 16 cm: MWU = 14.0, ns) (Figure 3.39).

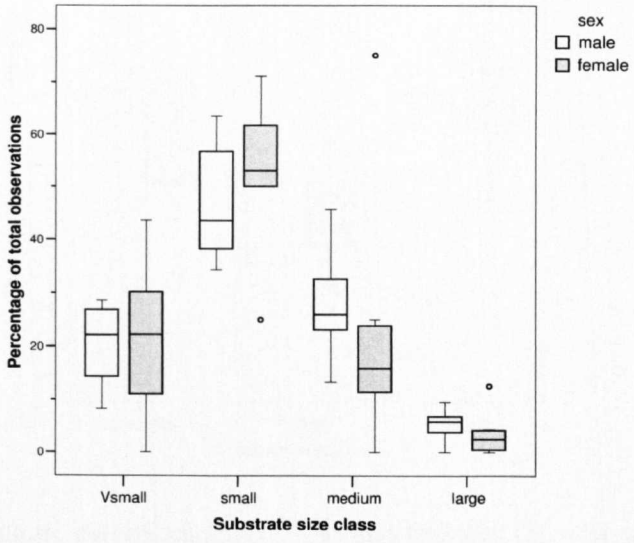


Figure 3.39. Percentage use by males (N = 9) and females (N = 8) of substrates of different diameters: very small (< 5 cm), small (6 – 10 cm), medium (11 – 15 cm), large (> 16 cm). The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

Substrate orientation

Overall, lorises used vertical substrates less frequently than horizontal or oblique substrates, which were used with equal frequency (Table 3.25).

Table 3.25. Percentage use of substrates of different orientations by lorises (N = 17) in MPFR.

	Substrate Orientation		
Descriptives	Horizontal	Vertical	Oblique
Median	40.0	22.0	40.0
Minimum	22.2	4.4	25.0
Maximum	51.1	50.0	55.0
Interquartile range	12.6	10.1	8.3

There was no significant difference between males and females in the frequency with which they used horizontal, oblique or vertical substrates (Horizontal: MWU = 13.0, ns; Vertical: MWU = 20.0, ns; Oblique: MWU = 18.5, ns) (Figure 3.40).

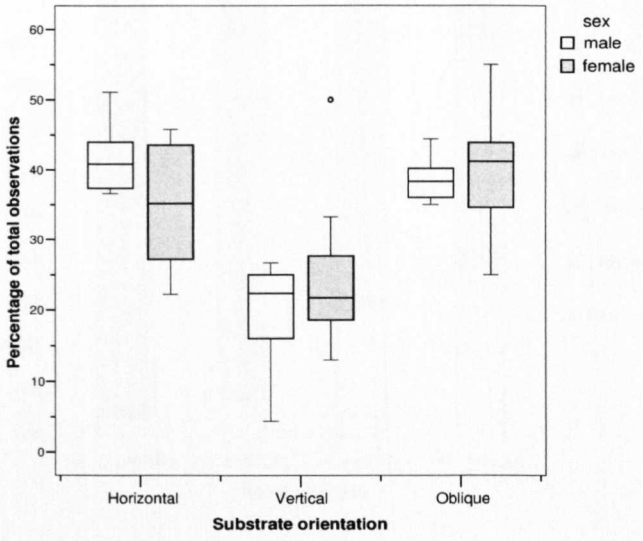


Figure 3.40. Percentage use by males (N = 9) and females (N = 8) of substrates of different orientation: horizontal, oblique and vertical. The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

3.6.4. Microhabitat use and activity

3.6.4.1. Plant species and activity

Sample size was too small to allow statistical analyses but descriptive data suggest that *Ochlandra stridula* and *Dillenia retusa* were used predominantly for foraging/exploring activities, whilst *Humboldtia laurifolia* and *A. nobilis* were used at approximately equal frequencies for grooming/resting activities and foraging/exploring activities (Figure 3.41).

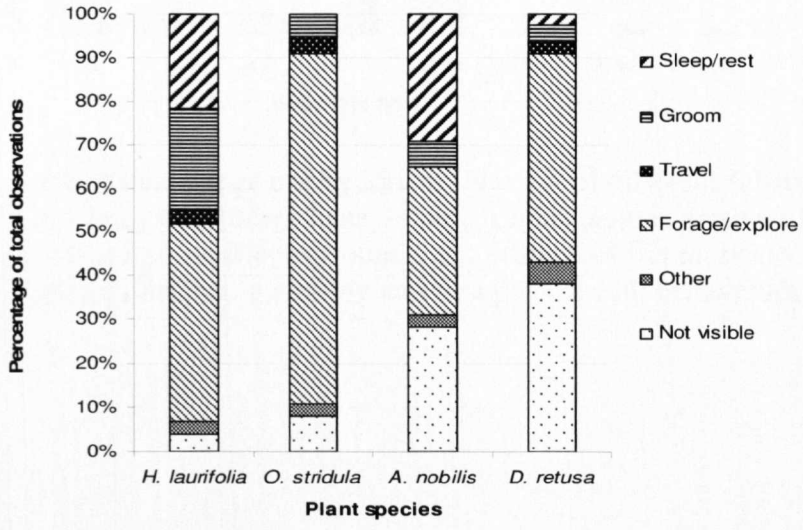


Figure 3.41. Distribution of behaviours across the four most frequently used dominant plant species (*Humboldtia laurifolia*, *Ochlandra stridula*, *Artocarpus nobilis* and *Dillenia retusa*) by lorises (N = 17).

3.6.4.2. Substrate type and activity

Lorises preferred branches for all types of activities. Nevertheless different substrate types were used at different frequencies according to the activity they were engaged in (Figure 3.42). Thus, branches were used mainly for activities that involved resting, sleeping and grooming, whereas lianas were mainly used for travelling and terminal

branches, trunks, bushes, dead trees and ground for foraging. The latter three were only used for the purpose of foraging.

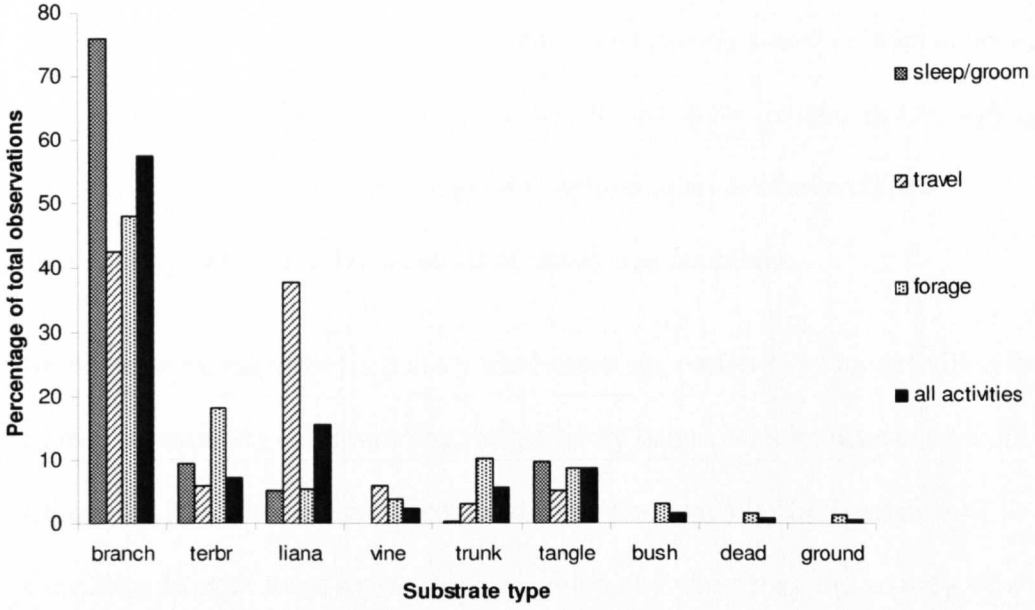


Figure 3.42. Average percentage use by lorises (N = 17) of different substrate types: branches, terminal branches (terbr), lianas, vines, trunks, tangles, bushes, dead trunks or branches (dead) and groundfloor (ground), according to different behavioural categories (sleeping/grooming, travelling and foraging) and all behavioural categories (all activities).

Summary

- Lorises were more frequently sighted in areas within MPFR characterised by *Humboldtia laurifolia* dominance, short trees measuring between five and 10 metres and relatively high level of disturbance. Lorises never used actively managed plantations such as rubber and pine, agricultural fields such as rice paddies or cinnamon, or home gardens. Lorises did use regenerating plantations and patch perimeter habitat. They used the latter significantly more than was available within their home ranges. However, lorises used interior forest habitat significantly more than edge habitat or regenerating plantations.

- Of all plant species recorded in MPFR (and their IVI calculated) lorises used the eight most dominant species on average 58.6 % ± 43.4 of the time. Of those eight dominant species *H. laurifolia*, *O. stridula* and *D. retusa* accounted for 45.2 % ± 41.3 of total observations. Lorises were most frequently found at heights between three metres and eight metres but were also found on the ground and as high up as 15 metres. Lorises were most frequently sighted in areas of overall low connectivity but where the presence of lianas was abundant.

- Branches were the most frequently used substrate, particularly for activities such as resting, sleeping and grooming, followed by lianas, which males used more frequently than females, and were used more frequently by both sexes for travelling. Lorises were shy to use the ground and when they did so they would remain within close proximity to a liana on the ground. Small substrates were used more frequently than very small, medium or large substrates. Horizontal and oblique substrates were used equally frequently and more than vertical substrates.

3.7. INFLUENCE OF ABIOTIC FACTORS ON BEHAVIOUR

3.7.1. Effect of rainfall, temperature and moonlight on activity

I used multiple regression analysis to test which independent variable (rainfall, temperature and NII) most significantly explained the variance in activity scores. Preliminary analyses were performed to ensure no violation of the assumptions of normality, linearity and homoscedasticity. The model, which includes temperature, rainfall and NII, explained 21.3% of the variance in activity scores ($r^2 = 0.224$, F (3, 46) = 4.433, p = 0.08). Of these three variables, temperature made the largest and

most significant contribution (beta = 0.421, p = 0.02). The other variables did not contribute significantly. Figure 3.43 shows rainfall and temperature patterns between August 2005 and June 2006, when the 13 radio-collared animals were tracked.

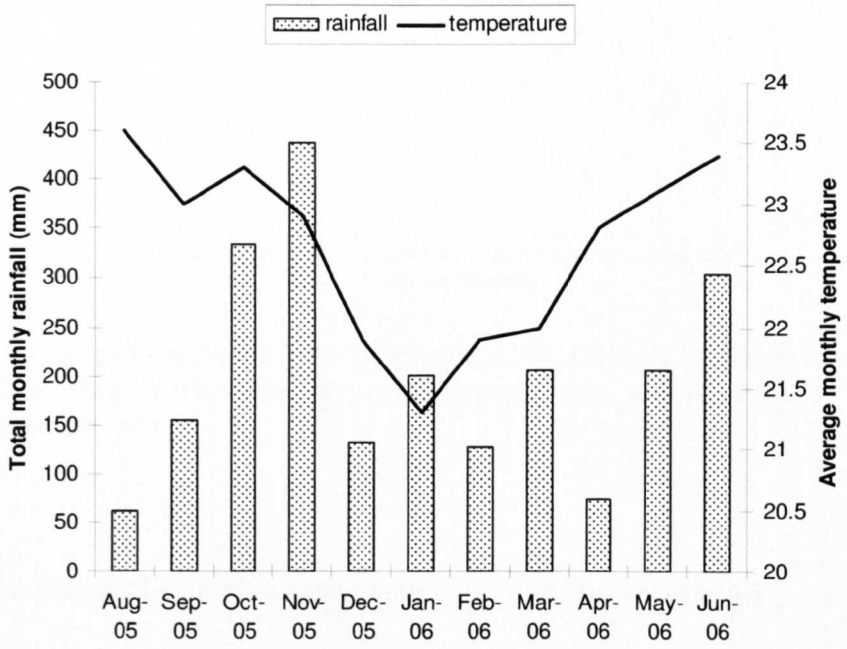
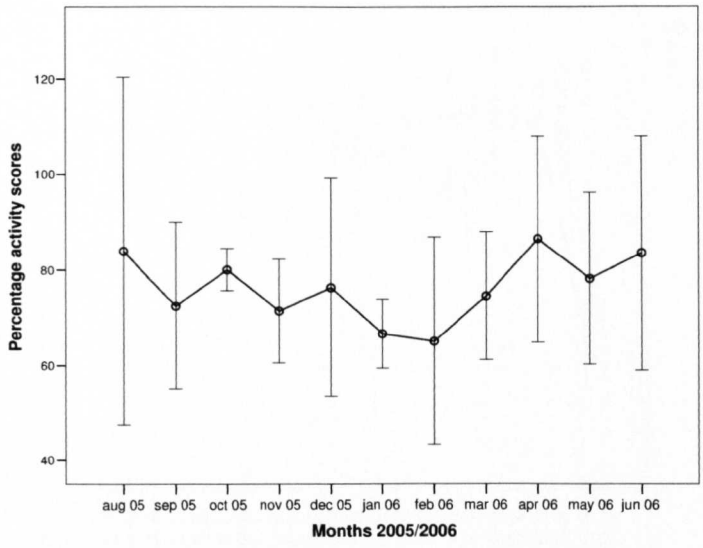


Figure 3.43. Rainfall and temperature patterns during the radio-tracking period (August 2005 to June 2006).

The activity pattern of radio-collared individuals is similar to that of the average monthly temperature pattern shown in figure 3.43 whereby activity decreases between the months of December and March when temperature drops. Despite the non-significant results of the regression analysis for the rainfall variable, this graph shows that the months with the lowest rainfall (August 2005 and April 2006) coincide with months of highest recorded activity, suggesting that activity may have increased with a decrease in rainfall (although the high inter-individual variation shown on Figure 3.44 for those months should be noted).



3.44. Monthly activity pattern of radio-collared individuals (N = 13) between August 2005 and June 2006. Values represent average percentage activity scores (± SD) for each month of the year.

The contribution of NII on variance in activity was further tested during the colder months of December, January, February and March when foliage biomass is reduced. During those months only, the model explained 37.8% of the variance ($r^2 = 0.224$, F (3, 16) = 3.244, p = 0.05) and of the three variables, temperature and NII made the largest and most significant contribution to the variance in activity (beta = 0.524, p = 0.024 and beta = -0.510, p = 0.033, respectively).

The pattern of activity across the night is similar on dark nights and bright nights (Figure 3.45), but overall (when activity scores for each hour of the night are averaged), average percentage activity scores for lorises (N = 12) were lower during bright nights (Median = 72.7; IQ range = 22.8; Min = 6.3; Max = 100.0) than during dark nights (Median = 82.2; IQ range = 19.9; Min =14.3; Max = 100.0) (Wilcoxon signed ranks test: z = -2.97, N = 13, p = 0.003)[3] (Figure 3.45).

[3] These statistical results are significant at p = 0.004 when a Bonferroni correction is applied.

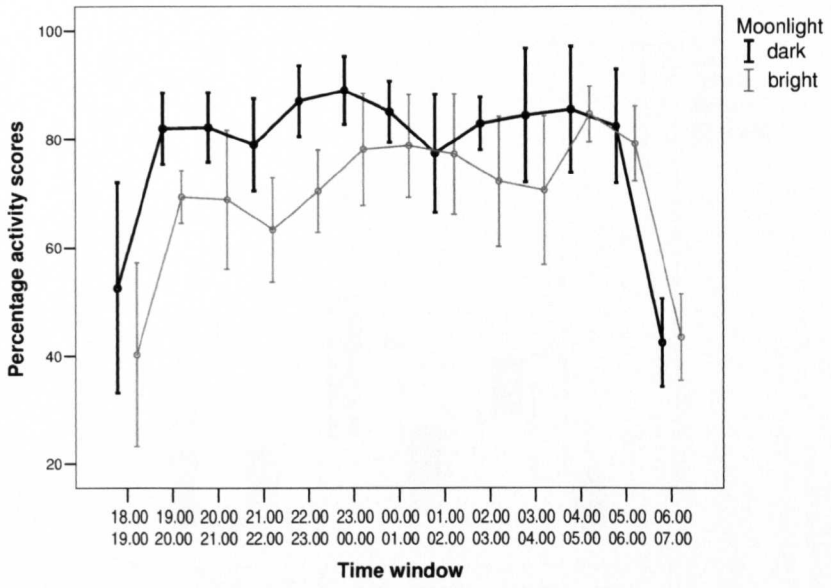


Figure 3.45. Difference in percentage activity scores for 12 lorises (six females and six males) for each hour of the night, between dark nights and bright nights. Values represent mean activity scores (mean obtained for each loris) $\pm$ 2SEs.

I tested for differences in frequency with which different behavioural categories (sleep/rest, groom, forage, travel, explore, and other) were recorded during dark nights and during bright nights. Sleeping/resting and grooming were recorded significantly more during dark nights[4], whilst differences for other behaviours were not significant (Table 3.26) (Figure 3.46).

Table 3.26. Results of MWU test looking at difference in percentage of observations of different behavioural activities between dark nights and bright nights.

	Sleep/ rest	**Groom**	**Travel**	**Forage**	**Explore**	**Social**
	n_1: 11	n_1: 12	n_1: 12	n_1: 12	n_1: 12	n_1: 11
	n_2: 11	n_2: 12	n_2: 12	n_2: 12	n_2: 12	n_2: 11
U	28.0	33.5	56.0	55.0	59.0	47.0
z	-2.15	-2.23	-0.62	-0.68	-0.75	-0.56
p	0.03	0.02	0.57	0.53	0.48	0.61

[4] These statistical results are not significant at p = 0.01 when a Bonferroni correction is applied.

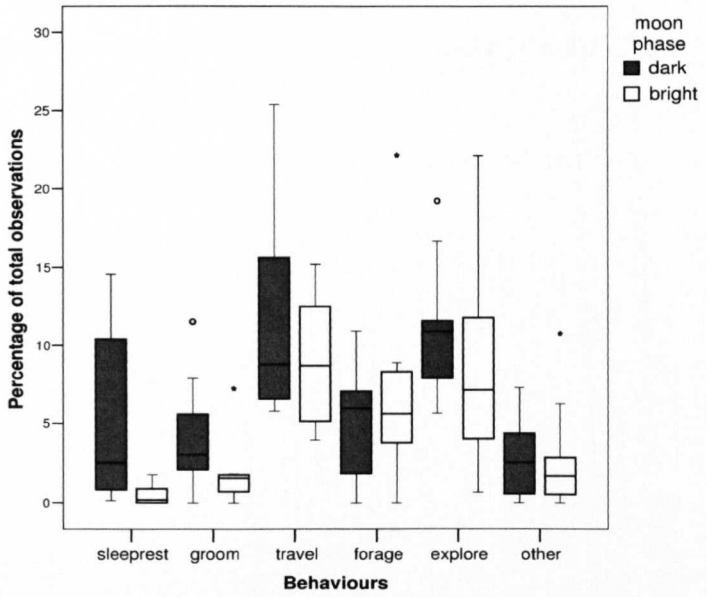


Figure 3.46. Comparison of the percentage of total observations during which lorises (six females and six males) were recorded in different behavioural categories (sleeping/resting, grooming, social, travelling, foraging and exploring) between dark nights and bright nights. The bar in each box represents the median value and the lower and upper edges of the boxes represent the lower (25%) and upper (75%) quartiles, respectively. The whiskers represent the maximum and minimum values.

3.7.2. Effect of rainfall and temperature on ranging patterns

The home range sizes of 12 individuals (six females and six males) were used to calculate monthly variation in home range size and mean nightly path length between August 2005 and June 2006 (see Figures 3.27 and 3.28 in Section. 3.5.8.2). The assumptions for linear regression analysis were not met for this data set. Therefore Spearman's rank order correlation analysis was conducted to test whether changes in temperature and/or rainfall were correlated with changes in nightly path length and home range size. There was a strong significant negative correlation between monthly home range size and monthly rainfall, whereby large home range sizes were associated with low rainfall levels (r = -0.636, n = 11, p = 0.035) (Figure 3.47). Variations in temperature did not correlate with variations in home range size (r =

0.046, ns). Additionally no significant correlation between nightly path length and rainfall and temperature was found (r =0.027, ns and r = -0.027, ns).

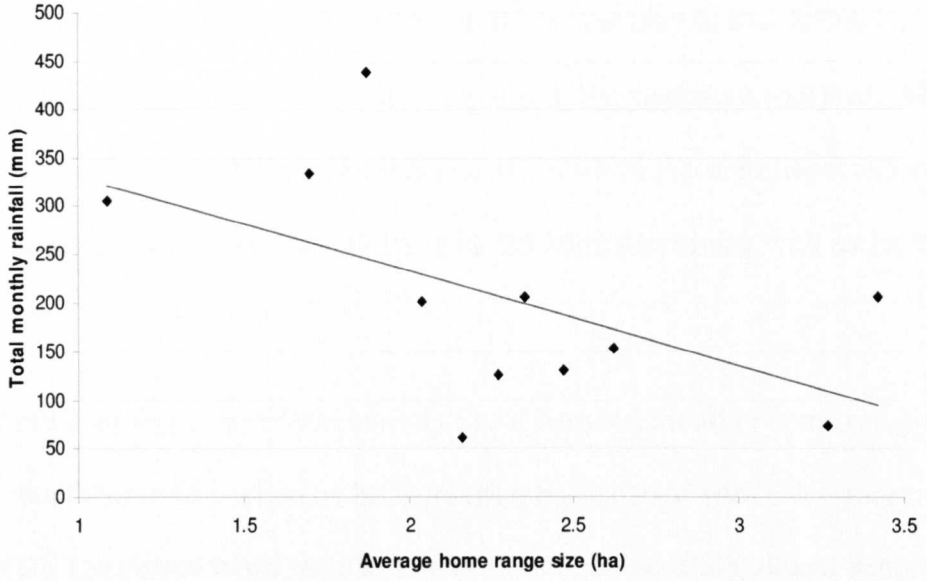


Figure 3.47. Trend in home range size against rainfall. Each data point represents the average monthly home range of individuals tracked in each of the 11 months, against total rainfall for each month.

3.7.3. Effect of moonlight on vocalisations

Based on a sample size of 1705 whistles (out of a total sample size of 1720 calls, 15 of those did not have information on moon luminosity) and 323 nights, lorises uttered the whistle at an average of 1.40 calls per hour (± 2.08) and a maximum of 12.14 calls per hour on bright nights (N = 165), and at an average of 1.21 calls per hour (± 1.36) and a maximum of 5.80 calls per hour on dark nights (N = 158). There was no significant correlation between the NII and the number of whistles uttered (r = -0.158, ns).

Summary

- Multiple regression analysis revealed that out of the three independent variables (rainfall, temperature and NII), temperature was the only one which had a significant effect on activity when all months of the year were analysed. When the drier and colder months only were analysed, an additional significant association was found between NII and activity, with the latter decreasing with an increase in NII.

- A significant negative correlation was found between monthly home range size and monthly rainfall, whereby home range size increased with a decrease in rainfall. Temperature had no effect on home range size. Rainfall and temperature did not affect nightly path length. Moonlight had no effect on calling rate.

- Lorises were significantly less active during bright nights than during dark nights but no significant difference was found in calling rate between dark nights and bright nights.

CHAPTER 4 GENERAL DISCUSSION

In this chapter I will discuss the results described in Chapter 3 in relation to the main aims of this thesis, which were:

1. To describe the study population and MPFR. I focus in this discussion on comparing density and abundance estimates obtained in this study and in previous surveys. I also evaluate the conservation value of MPFR.

2. To investigate the social organisation of *L. t. tardigradus*. I use quantitative data on social and spatial patterns to infer the social organisation and associated mating system of this species. I compare this to the social organisation exhibited by *L. lydekkerianus*.

3. To evaluate the degree of behavioural and ecological plasticity exhibited by *L. t. tardigradus* based on observed patterns of habitat and microhabitat use and responses to abiotic factors.

4. To propose conservation goals for *L. t. tardigradus* and avenues for future research based on the findings from the first three aims of this study.

4.1. THE STUDY POPULATION AND STUDY SITE

4.1.1. Slender loris abundance estimates

I estimated slender loris encounter rate at MPFR to be 0.70/km in 2005, across an area measuring approximately 100 hectares and an encounter rate of 1.06/km across the area surveyed in previous years measuring approximately 25 hectares (Nekaris and Jayewardene, 2004). In 2001, Nekaris and Jayewardene (2004) estimated the encounter rate to be of 13 animals per kilometre, 3.85/km in 2002 (Nekaris and

Jayewardene, 2004) and 1.1/km in 2004 (Nekaris, unpublished data). Slender loris density, estimated using the line transect method, was reported to be 0.24/ha in 2004 (Nekaris, unpublished data), whilst in this study I estimated a density of 0.48/ha based on the number of animals caught and their conspecifics and infants.

Although the slender loris population appears to have decreased between 2001 and 2005, it seems unlikely that it would have decreased so dramatically between 2001 and subsequent years. It seems more likely that differences in methodological aspects may have resulted in such disparate figures. In surveys conducted in 2001, less than 20kms were walked and surveys were restricted to the area SS2, reported in this study as having the largest density of lorises (0.9/ha) compared to other areas in MPFR (0.33/ha and 0.17/ha). The short survey time and restriction to an area of high density, coupled with the possibility that surveys were conducted at a time where loris activity may have been relatively high (such as during dark moon phases or a mating period; See results in sections 3.1.3 and 3.5.7.3 respectively), would all contribute towards a biased estimate (particularly in 2001 when only a small area of MPFR was surveyed). The fact that density estimates obtained in this study are double those obtained from surveys conducted the previous year also suggests that the use of line transect methods may result in an underestimate of density. However, surveys in 2004 (Nekaris, unpublished data) were conducted over a relatively shorter period of time, which may again have resulted in such different density estimates. On the other hand, short surveys conducted on *Nycticebus* sp. have yielded good density estimates (Nekaris, unpublished data). The slight decrease in slender loris density also may be a result of fluctuations in population densities from year to year as some years more births than deaths may occur and vice-versa. However, it also is likely that the density of lorises at MPFR has decreased as a result of a decrease in forest extent. I showed

that in less than 50 years, MPFR decreased by just over 50%. Although such decrease appears to have occurred primarily between 1968 and 1985, the decrease in forest extent since 1999 also suggests that MPFR may continue to decrease, resulting potentially in a further decrease in loris population density.

Pine forest plantations found around MPFR and other forest patches within the Wet Zone, were set up in the 1970s to act as buffer zones by preventing further encroachment into the forest by surrounding communities. Currently, the Forest Department owns approximately 1700 hectares of mature pine plantations in Masmullah, Dandeniya, Kakunadura and Aparekka areas, of which 200 hectares were released in 1995 to the Environment Conservation Foundation (ECF) to extract pine resin, which provided families around MPFR with a monthly wage of approximately Rs. 5000 (Rushini, pers. comm.). However, the completion of the tapping cycle and over maturity of pine trees resulted in the tapping operations being interrupted by the Forest Department in 2004 and the subsequent unemployment of tappers (of whom 95 per cent were women). During the period of pine tapping, people protected the forest for the benefits it brought. However, since 2004 pine plantations have been destroyed by villagers mostly by setting fire to them and by encroaching on the land for other uses. I have shown that lorises made use of regenerating pine plantations and through the recent destruction and encroachment into abandoned plantations, lorises are losing potential habitat. However, despite the numbers appearing to be relatively low and potentially on the decrease, the slender loris population at MPFR appears to be the most abundant of all patches surveyed in the Wet Zone (Nekaris and Jayewardene, 2003; Gamage, pers. comm.). The possible reasons for this are discussed in Section 4.3. Considering that *L. t. tardigradus* is currently listed as Endangered by the IUCN

(2008), makes MPFR and its surrounding area, in need of conservation action to prevent further encroachment. I discuss this further in section 4.4.1.

Much of the forest where the study population was situated was isolated from other parts of MPFR where other lorises were found. However, some connecting points may have been used by lorises to disperse across the forested areas within MPFR but not without some degree of difficulty. Entry points for many of the lorises (those whose home ranges were furthest away from the nearest entry point), would require considerable travelling (long distances of more than three times the diameter of their normal home range) along an extensive network of paddy fields before finding an entry point allowing access to other forest parts. In addition, much of the study site was separated by pine forest plantations, which lorises did not use unless the plantations had been abandoned and left to regenerate, thus providing undergrowth (in the form of tall grasses, bushes, saplings) that could potentially be used by lorises to cross the plantation without having to walk on the ground. The stream, which also fragmented much of the forest, was too wide for the canopies of trees along the edge to connect. However, in some cases fallen trees, bringing down with them tangles of lianas and branches, could be used as a bridge to cross the stream. Additionally, some parts of the stream were narrower and in those cases, the canopy of the trees could theoretically connect and allow lorises to cross. Finally, there was an area that connected that side of the forest with the other side but unfortunately it consisted of the grounds of the Buddhist monastery (see Figure 2.5), which not only provided little arboreal connectivity (but not completely absent) but also had a large number of domestic cats and dogs, which may have been seen as a threat by lorises. No lorises were ever reported to come to the grounds of the monastery but lorises were known to occur on the edge. We were not permitted to survey the area due to the disturbance

this would cause the monks at night and for other reasons related to religious beliefs. Thus, this possibility cannot be ruled out and the monastery grounds remain a potential access point for lorises. In conclusion, the study population cannot be considered a completely closed population as there was some potential for dispersal, albeit small.

When a population is said to be isolated or in this case open but with limited potential for dispersal to other parts of MPFR, one must consider whether this population is viable or not and whether it should be referred to as a source or a sink population. Whether the study population is a source (of individuals to other parts of MPFR) or a sink would depend on the level of immigration to the focal population from the population on the other side of the study site. A sink population by definition (Hanski, 1999) would go extinct in the absence of immigration. For the study population to be referred to as a source population, it would need to show positive growth rates and be the source of emigrants. Since the population inhabiting the other part of MPFR was not studied and no data were obtained on emigration/immigration patterns between areas of the forest, the nature of the study population as a source or sink cannot be ascertained. As a whole, the population of MPFR can be said to be closed since no opportunity for movement between MPFR and neighbouring patches exist. However, whether the MPFR population will go extinct in the absence of immigration cannot be determined at this stage. It may be that the quality of the habitat in MPFR is good enough to allow positive growth rates to occur, thus making this population a source rather than a sink population. Further studies looking at patterns of movement within MPFR and the reproductive rates of different populations within the forest are needed to better understand the dynamics of the MPFR population.

4.1.2. Biodiversity of MPFR

Even though Sri Lanka has been declared as one of the 25 'biodiversity hotspots' of the world (Myers *et al.*, 2000) relatively little of its biodiversity, which is concentrated in the Wet Zone (Crusz, 1986; Erdelen, 1988), has been documented and published. This lack of knowledge of what Sri Lanka's remaining Wet Zone forests hold has been a major drawback in conserving the biodiversity of Sri Lanka (Weerakoon, 2001). Although some biodiversity surveys were conducted in MPFR by the Department of Wildlife and Forest Department, such information is not made available. In addition, surveys are not repeated, resulting in a lack of knowledge of extinction rates for fauna and flora species of the Wet Zone. There is belief that some species have already become extinct due to lack of conservation efforts, such as the two species of fish, *Labeo lankaei* and *Macrognatus aral* (Weerakoon, 2001). The IUCN Red List of Threatened Species has been a valuable tool in identifying the conservation status of species but without baseline data the conservation status of many species cannot be assessed accurately (IUCN, 2008). Although I focussed only on a small fraction of the fauna at MPFR, I nevertheless was able to report the presence and abundance of several mammal species, which helps provide a platform for future surveys (Strayer, 1999).

Despite MPFR being classified as a Proposed Forest Reserve, little conservation effort has been made towards monitoring changes in its faunal diversity and species population numbers. As a forest MPFR appears to hold an important mammal population, with most of these species being classed as Vulnerable or Endangered. All of Sri Lanka's Wet Zone primate species, as well as several viverrids and felids were found in MPFR. The presence of other mammals such as the mongoose, the otter and the porcupine, also contribute towards the conservation value of this forest.

Additionally, knowledge of the ecological needs of species can act as a valuable tool in identifying the 'health' of a habitat and subsequently make appropriate conservation plans. In Malaysian Borneo, mouse deer (*Tragulus javanicus*) density has been positively correlated to availability of potential food resources such as fruiting trees; in particular *Ficus* trees, and negatively correlated with the proportion of severely disturbed forest (Heydon and Bulloh, 1997). In MPFR, mouse deer was the second most abundant species, suggesting that food availability is high enough and disturbance low enough to allow populations to remain relatively high. Whether the calculated encounter rate of the mouse deer in MPFR reflects a healthy population remains to be investigated as no other published study reports densities of frugivorous ungulates in Sri Lanka (including the muntjac, *Muntiacus* spp.). Nevertheless, *Moschiola kathygre* has recently been recognised as a distinct species (Groves and Meijaard, 2005) and classified by the IUCN (2008) as Vulnerable with population numbers declining, suggesting that this relatively recently recognised species is in need of conservation effort, as is any forest it inhabits. MPFR also was inhabited by two of Sri Lanka's primates, the purple-faced langur and the toque macaque, both listed as Endangered (IUCN, 2008). The numbers of these primates are declining as a result of habitat reduction (Molur *et al.*, 2003) and forests like MPFR need to receive more attention and be the site of further biodiversity surveys in order to monitor how the primate populations fare over time.

Other endangered species recorded in MPFR include the fishing cat (*Felis viverrina*) whose numbers have declined by 50% in the last two decades (IUCN, 2008). It has become extinct in the past five years from certain parts of Southern India and Pakistan, and if no conservation efforts towards protecting its habitat and this species are made, it may become extinct from Sri Lanka too. Currently there are no records of

this species' distribution or population numbers in Sri Lanka, except for one record by Nekaris (IUCN, 2008). Other species recorded include the golden palm-civet (Vulnerable) and the Indian brown mongoose (Vulnerable) (see Appendix 8 for exact IUCN listing for 2008) resulting in nearly 50% of the total number of mammal species recorded in MPFR being Vulnerable or Endangered. The principal aims of this study were not to conduct extensive biodiversity surveys of MPFR but merely to provide some clues as to the potential of this forest and its need for conservation efforts, and to provide a springboard for future surveys in MPFR and surrounding forest patches.

Little data on abundance estimates and/or densities of *Trachypithecus vetulus vetulus* and *Macaca sinica aurifrons* are available for comparison with this study. A study I conducted in 2003 on a 41 hectares regenerating lowland rain forest patch in the Galle District of Sri Lanka's Wet Zone (Bangamukande Estate, BKE), reported abundance estimates of 0.13grps/km and 0.14grps/km for *T. v. vetulus* and *M. s. aurifrons*, respectively. These figures are lower than those obtained in this study, particularly for the purple-faced langur (0.23 grps/km and 0.16grps/km). Unlike MPFR, the BKE forest patch was entirely exploited for mono-crop plantations, which were eventually abandoned and the forest left to regenerate naturally. Although the study revealed a relatively high faunal and floral diversity (Bernede, 2003), populations of most mammal species, including the primates, occurred at very low densities, which is possibly related to forest patch size, habitat degradation and fragmentation, and hunting (Bernede, 2003). MPFR on the other hand is a larger and less disturbed forest patch where hunting was never witnessed or reported during the two year study period. Unlike BKE though, which is 'attached' to a large primary rainforest (Hiniduma Reserve) via a network of privately owned estates similar to BKE and thus

offers the possibility for those populations to disperse to better habitat, MPFR is isolated from primary rainforest patches and surrounded by urban landscapes. However, unlike the slender loris, the langur and macaque species are able to travel through home gardens and subsist off anthropogenic landscapes occurring between forest patches (Parker *et al.*, 2008), making populations of these primate species less susceptible to the effects of fragmentation and thus in theory more viable than loris populations. On the other hand, local extinctions of *T. v. nestor*, resulting in a decline of 80% (IUCN, 2008), have been documented in the more anthropogenically disturbed western provinces of Sri Lanka making this subspecies Critically Endangered (IUCN, 2008). In addition, studies conducted by Nekaris (unpublished data) on more than 30 forest patches in the Wet Zone report figures of 0.33 animals/km^2 and 0.17 animals/ km^2 for *T. v. vetulus* and *M. s. aurifrons*, respectively, both of which reflect low population densities and the vulnerability of these species. Should the rest of Sri Lanka's southern provinces follow the same course of urban development occurring in the western provinces inhabited by *T. v. nestor*, a similar fate awaits the already Endangered *T. v. vetulus* and *M. s. aurifrons*, both of which are not tolerated by humans (Molur *et al.*, 2003, in IUCN, 2008).

4.2. THE SOCIAL ORGANISATION OF *LORIS TARDIGRADUS TARDIGRADUS*

In this section I discuss the findings on the spatial system and social system of *Loris tardigradus tardigradus* to elucidate the social organisation of this primate. It has become clear over the last decade of intensified research on prosimians that not only do nocturnal primates exhibit greater complexity and variation in their social organisation than had previously been reported (Gursky, 2000, 2002; Sterling *et al.*,

2000) but that greater intra-specific variations are starting to emerge, as has been shown in mouse lemurs (Kappeler *et al,.* 2002; Wimmer *et al.*, 2002; Radespiel, 2000) and tarsiers (Gursky, 2000, 2002; Merker, 2006). Social organisation can be described as comprising three components: the spacing system, represented by the spatial and temporal distribution of individuals, the social system, described by the behaviour and relationships between individuals within a group, and finally, the mating system, defined by the reproductive interactions between individuals (Sterling, 1993).One of the aims of this study was to provide the first clues of the social organisation of *L. t. tardigradus* by quantitatively assessing its spatial and social system and obtaining some preliminary qualitative data on its mating system.

Although models of social organisation such as that by Bearder (1987) and Mueller and Thalmann (2000) allow for a practical definition of an animal's social organisation and thus comparison with other species, what is observed in the wild may not always correspond neatly to the categories of these models. Nekaris (2003a) attempted to describe the social organisation of *Loris lydekkerianus lydekkerianus* using the definitions of social organisation by Mueller and Thalmann (2000). She found that the patterns of spatial behaviour exhibited by *L. l. lydekkerianus* most resembled the multimale spatial patterns described by Mueller and Thalmann (2000) but their social behaviour did not fit neatly into their three categories (solitary, dispersed or gregarious). Instead their social system was described as dispersed but with a degree of gregariousness higher than reported for most nocturnal primates (Nekaris, 2003a, 2006). Similarly, the patterns of spatial and social behaviour described by Kar Gupta for *Loris lydekkerianus malabaricus* do not conform to one category (of spatial system and social system) in particular. Despite Kar Gupta (2007) describing the social organisation of *L. l malabaricus* as unimale-unifemale with a

dispersed social system (solitary foragers with social networks), the degree of variation within the population suggests a much more complex social organisation, with regards to within-population differences in inter-individual interactions and group cohesion.

In this discussion I attempt to fit my findings into the model of social organisation defined by Mueller and Thalmann (2000). I discuss these findings in relation to what is known on the social organisation of other loris taxa and the environmental pressures faced by lorises at MPFR.

4.2.1. The spatial system

In the results (section 3.2) I showed that:

1. Despite females having slightly larger home ranges than males, there were no significant inter-sexual differences in home range size.
2. The home range of a male extensively overlapped the home range of one female
3. Male-male overlap was smaller than female-female overlap
4. Females overlapped with more females than males did with males.
5. Both adult males and females were able to defend their home ranges, but not dispersing subadults.

How do these findings relate to what we know on the social organisation of other slender loris taxa? In the case of *L. l. lydekkerianus*, males had larger home ranges than females and thus overlapped the home ranges of more than one female. Males also overlapped home ranges of other males whilst females had little overlap with

other females (Nekaris, 2003a, Radakrishna, 2002). In the case of *L. l. malabaricus*, Kar Gupta (2007) suggests a unimale-unifemale system, even though males had on average larger home ranges than females. This classification may have been based on the fact that amongst males, there were settled and paired males, whose home ranges overlapped more with that of one female than with any other female. Males with larger home ranges, the roaming males or the settled but unpaired males, did not share their home range exclusively with one female. Unlike *L. l. malabaricus, L. t. tardigradus* showed no male-male differences in home range size. However, some males were more settled than others based on the fact that they regularly slept with the same female, shared her sleeping sites and interacted with her more than with any other female. In addition, the home ranges of sleeping partners overlapped more than home ranges of non-sleeping partners, as observed with *L. l. malabaricus* (Kar Gupta, 2007) and *Microcebus murinus* (Radespiel, 2000). As in *L. l. malabaricus* (Kar Gupta, 2007) these ranging patterns would be characteristic of a unimale-unifemale spatial system, rather than a multimale-multifemale system as seen in *L. l. lydekkerianus* (Nekaris, 2003a, Radakrishna, 2002). This also is similar to the spatial system exhibited by other lorisines, such as *Perodicticus potto* (Pimley *et al.*, 2005), *Nycticebus coucang* (Wiens, 2002) and other nocturnal prosimians, such as *Tarsius spectrum* and *Galago zanzibaricus* (Bearder, 1987).

4.2.2. Range movements and defendability

Lorises at MPFR travelled far greater distances than did the larger *L. l. lydekkerianus*, whose nightly path length averaged 90.0 m (± 42.0) for males and 106.0 m (± 26.0) for females. The rapid locomotion of *L. t. tardigradus* (Nekaris and Stevens, 2005) would allow such large distances to be covered, but the question remains as to why

lorises at MPFR would travel such far distances (in comparison to *L. l. lydekkerianus*).The difference between *L. t. tardigradus* and *L. l. lydekkerianus* may be down to environmental differences. Whereas the dry deciduous forests of Tamil Nadu (India) provided easily locatable patches of abundant resources (Nekaris, 2000), it may be that at MPFR, resources are more patchily distributed and/or less plentiful, which may result in animals having to move around more in order to obtain sufficient resources from various feeding sites. Alternatively, as a result of the relatively high density of lorises within such a small patch, competition for resources is high, resulting in lorises at MPFR travelling longer distances to defend territories.

The high values obtained for indices of territoriality (the index of defendability (D) (Mitani and Rodman, 1979), the range traversing index (RTI) (Martin, 1981) and the fraction monitoring index (M) (Lowen and Dunbar, 1994)) indicate that both males and females in MPFR are able to defend their territories (as opposed to home ranges that are not defendable (Morse, 1980)). The low degree of intra-sexual overlap and inter-sexual overlap between animals not forming a pair, supports the idea that lorises at MPFR showed a certain degree of territorial defense (Cheney, 1987), which may have been cooperative in nature for pairs, as with *Tarsius. spectrum* (Niemitz, 1979, in Bearder, 1987). The fact that males and females both defended their territories may be indicative of high competition for resources. However, results on social interactions between animals and the lack of wounds noted on caught animals, show that very few direct negative interactions (such as fighting) occurred and that instead territory defense was passive rather than active. I discuss this further in the next section.

4.2.3. The social system

4.2.3.1. Inter- and intra-sexual interactions, cohesiveness and territorial defense

The majority of social interactions observed were between males and females. Intra-sexual interactions were less frequent, particularly between males, who interacted with fewer males than did females. Female interactions occurred in several contexts, including a dispersing female encroaching into the territory of another female and whistle calls being exchanged between the two with the 'resident' female initiating the calls and calling more frequently. The dispersing female would either move off to a new area, as was the case for FG, or remain on the edge of the 'resident' female's territory, as did FB. Other contexts in which females interacted included neutral interactions whereby females tolerated each other and moved independently of the other. On one occasion, females FI and FK, were observed foraging within five to 10 metres of each other, along the boundaries of their respective territories, which overlapped by less than 10%. Interestingly though, these two females show a slightly negative degree of cohesiveness, suggesting a slight tendency to avoid each other. They did not appear to have direct interactions, such as grooming or playing, or aggressive interactions, such as fighting or chasing each other off, which once again supports the idea of passive territory defense. Other females whose territories overlapped slightly, such as females FB and FE, and FI and FE, moved independently of each other but on some occasions could be found within 20 metres of each other, where their territories overlapped. They never interacted directly and moved independently of each other.

Six radio-collared males were seen interacting with each other in this study and non-collared males were observed interacting when a female was in oestrous. On such occasions, there would be more than one male present (two to five) and they would chase each other and attempt to mate with the female. Fights were rare but vocal exchanges were frequent on such occasions (up to 30 per hour). In situations other than when a female was in oestrous, encounters between males were not observed frequently and were either neutral or agonistic. Radio-collared males MJ and MA had slightly overlapping territories (< 5%) and were seen within 20 metres of each other on several occasions. Ma was caught whilst tracking MJ and at the time was about 20 metres away from MJ. However, they showed low levels of cohesiveness, moving independently of each other and not showing any sign of agonistic behaviour. Males MT and MJ and MA and MJ, on the other hand, showed higher levels of cohesiveness, despite their territories also overlapping slightly (as with Ma and MJ). This may be explained by the fact that males MT and MA occasionally ventured into MJ's territory or moved along its boundary. Each time this happened MJ would travel along the boundary of its territory until the males moved away from the boundary (see Section 3.5.2). These interactions would explain the relatively high degree of cohesiveness (indicating that movements are dependent of each other) found between these two males (see Section 3.5.5).

In both cases described above (MJ-MT and MJ-MA) no vocal battles were exchanged (but calls by MJ were uttered whilst rapidly moving along its territory boundary, with no response from MA or MT) and no direct negative interactions were observed. Both males, MT and MA, only attempted to extend their own territory into that of the other male a few times but eventually gave up. Direct fights were never observed and vocal exchanges between males were rare.

Data on defendability indices (section 3.2.7.), and the low degree of overlap and interactions between non-group neighbours suggest that lorises at MPFR have territories to defend. However, the lack of direct fights between animals or signs of fighting on caught animals implies that territorial defense exists but is inconspicuous in nature (Morse, 1980). For a nocturnal mammal that relies heavily on its sense of smell, such as the slender loris (Schilling, 1979), scent-marking may be a safe way to defend one's territory or communicate one's dominance (Miller *et al.* 2003). Scent-marking for the purpose of defending territories has been observed in sifakas (*Propithecus verreauxi*: Jolly, 1966; Johnson, 1973), whilst scent-marking to communicate male dominance to other males has been observed in golden lion tamarins (*Leontopithecus rosalia*; Miller *et al.*, 2003), cotton-top tamarins (*Saguinus oedipus*: French and Cleveland, 1984) and saddle-back tamarins (*Saguinus fuscicollis*: Epple *et al.*, 1979) and scent-marking may have provided an effective form of communicating the male's status in MPFR. Females were as capable of defending their territories as males, with the exception of the subadult FG. Like males, both vocalisations and scent-marking were observed in context of potential territorial defense, although scent-marking was only recorded twice for females. Vocal exchanges between neighbouring animals occurred along territory boundaries when one neighbour attempted to encroach into the territory of the settled female. Scent-marking in general was rarely observed in MPFR. This may simply have been as a result in difficulty in detecting this behaviour when the animal was high up in the canopy, or may simply suggest that scent-marking is too costly for lorises at MPFR. The predators of lorises in MPFR were most likely palm-civets, who rely heavily on their sense of smell to detect prey. Scent-marks deteriorate over time, thus fresh marks by a loris would advertise its position quite efficiently. This may be too high a risk to

take, whereas the direction of a loris whistle call is difficult to discern. This may explain the high frequency of calling rate and low frequency of scent-marking in comparison to *L. l. lydekkerianus* where no predators occurred (Nekaris, 2000).

4.2.3.2. Sociality throughout the night

When studying the social organisation of any species, it is important that in addition to describing ranging patterns between individuals of a population, one should also describe the social interactions between individuals (Mueller and Thalmann, 2000; Whitehead, 1997; Sterling, 1993). Patterns arising from social interactions are more difficult to discern than ranging patterns (Lee, 1994) and this is especially true of cryptic animals or animals that do not form conspicuous groups but may interact through vocalisations or scent-marking (Whitehead, 1997). As a result, nocturnal primates have often been considered to have limited social interactions and thought to lead a rather solitary life (Kappeler, 1997a). We now know that patterns of sociality in prosimians are much more complex than previously thought and differ widely both between and within species (Pimley *et al.*, 2005; Schulke and Kappeler, 2003; Kappeler and van Schaik, 2002; Sterck, 1999).

Adult slender lorises at MPFR, including non-collared ones, were within 30 metres of other lorises 21.4% of observations, and within 20 metres of another loris, 18 % of observations. Table 4.1 presents figures of sociality reported for other prosimians species for comparison. The percentage sociality reported in this study is comparable to figures reported for other lorisids (e.g. *G. moholi* and *P. p. edwardsi*), whilst other lorisids appear less gregarious. The angwantibo (*Arctocebus aureus*) spent only 1 % of its time near another conspecific (Charles-Dominique, 1977). The maximum IID at

which two or more animals were said to be 'social' was not specified, but even if sociality was considered only when animals were less than five metres apart, this is still lower than the figure obtained in this study at that distance (6.2%). Lorises at MPFR also were more gregarious than the slow loris (*Nycticebus coucang*) at the maximum IID of 20 metres (6.7 % against 18 %). On the other hand, figures reported for other slender loris species are a lot higher (Nekaris, 2000; Nekaris, 2006; Nekaris and Jayewardene, 2003). A long term study on *L. l. lydekkerianus* in the dry thorny forests of Southern India (Nekaris, 2000) revealed that lorises were social approximately 41 % (with sociality defined as animals being within 30 metres of each other) and 38 % (when only interactions within 20 metres are taken into account) of total observations. Similarly, *L. l. nordicus*, also inhabiting dry, thorny scrub forests in northern Sri Lanka, was reported to be social 49.5 % of the time. These higher levels of gregariousness apparent in the slender loris forms inhabiting dry zone habitats (*L. l. nordicus* and *L. l. lydekkerianus*) in comparison to that exhibited by *L. t. tardigradus*, may reflect ecological differences, particularly with regards to the type, amount and distribution of available resources in the different habitats (I discuss this further in section 4.2.5 on the reasons for observed patterns of social and spatial interactions in *L. t. tardigradus*).

Table 4.1. Percentage sociality reported for other prosimian species. The maximum inter-individual distance (IID) used to define interactions as being social is reported against the percentage sociality recorded at that distance.

Species	Maximum IID (m)	Sociality (%)	Source
Loris tardigradus tardigradus	30	21.4	Current study
	20	18.0	
L. t. tardigradus	5	43.7	Nekaris and Jayewardene, 2003
L. lydekkerianus nordicus	5	49.5	Nekaris and Jayewardene, 2003
L. lydekkerianus	30	~ 41.0	Nekaris, 2000
lydekkerianus	20	38.0	Nekaris, 2006
Perodicticus potto edwardsi	20	21.8	Pimley, 2002
Nycticebus coucang	50	18.1	Wiens, 2002
	20	4.5	
Galago moholi	20	18.0	Bearder and Martin, 1980
Tarsius spectrum	20	40.0	Gursky, 2005
Arctocebus aureus	?	1.0	Charles-Dominique, 1977

The high figures reported for *L. t. tardigradus* by Nekaris and Jayewardene (2003) in comparison to those reported in this study, may reflect circumstantial differences between the two studies. Surveys were relatively short (120 survey hours) and conducted between March and May, during which time animals may have been more gregarious as a result of females being in oestrous (true but see below) (See section 3.5.8 for results on mating season). In addition, data were collected at point of first contact, which although has been shown to be comparable to data collected with instantaneous sample points (Nekaris, 2001), may have given slightly different results.

Thus, care must be taken when comparing these figures of sociality. Other difficulties related to comparing studies of sociality in prosimians relates to the different definitions of what constitutes a social interaction or when animals should be considered as being 'together', particularly with regards to inter-individual distance.

With the exception of the studies on the slender loris (Nekaris, 2000) where social interactions are reported at distances of up to 30 metres, the majority of studies examining sociality in prosimians class animals as being 'together' when they are within 20 metres or less of conspecifics (Table 4.1). It is therefore important that when examining sociality in nocturnal posimians, the percentage sociality should be reported at different distances so as to make comparison between studies possible.

Social interactions occurred at all times of night but were most frequently recorded around the sleeping sites (before animals moved off to forage or travel and after animals met up again to settle into their sleeping groups). Despite the decrease in percentage of social interactions observed after 20.00 and the increase after 06.00, around sleeping sites, social interactions nevertheless remained relatively high throughout the night. The majority of social interactions were neutral (> 50%), followed by indirect positive interactions (36.1%). Direct positive interactions were not frequently observed (7.9%), whilst negative interactions, whether indirect or direct were the least frequently recorded (3.5% and 0.4% respectively). For those animals that were not part of a stable sleeping group, such as the subadult female FG and females FI and FR, percentage sociality was relatively low, particularly in the case of FG (~4%).

It was not until relatively recently that nocturnal primates were considered solitary animals with little interaction outside the breeding season, despite some authors challenging this notion (Charles-Dominique, 1978; Bearder, 1987). Since then, numerous studies have reported levels of sociality not dissimilar to those seen in diurnal primates (Nekaris and Bearder, 2007). Schulke and Kappeler (2003) state that in order to constitute a group, animals sharing considerable space must exchange more social interactions with each other than with individuals with whom they share

only little space. Fuentes (2002) further adds that a social pair will be closer spatially than with other members of the population, including a non-dependent individual within the group. By that definition, lorises at MPFR appear to form groups consisting primarily of an adult male and an adult female and could be described as a social pair. According to Fuentes (2002) a "social pair bond is a long-term (> one year/seasonal cycle) association between two non-kin adults characterised by a set of partner-specific affiliative behaviours and/or energetic investment distinct from all other dyadic interactions engaged in by the two adults with other group members." (Fuentes, 2002:969). The results presented in section 3.5 shows that members of a 'pair' interact significantly more with each other than with any other members of the population, including lorises with which they share a smaller part of their home range, and show significantly higher levels of cohesiveness than non-pairs, extending to sleeping site locations. Grooming occurred exclusively between members of a spatial pair or sleeping group, and a male that was not part of a spatial pair or sleeping group was aggressively rejected by the female when an attempt to groom her was made (as described for male MA in Section 3.5.2). Data on vocalisations show that the majority of short-distance calls at dusk and dawn occurred between members of a pair, providing supporting evidence that lorises in MPFR form social pair bonds, as observed with the pair-living *Lepilemur edwardsi* (Rasoloharijaona *et al.*, 2005).

The degree of cohesiveness and the frequency of interactions throughout the night with other animals, and the sleeping associations, varied within the population making it difficult to fit them into a specific category, as observed with *Loris lydekkerianus malabaricus* (Kar Gupta, 2007). The variation in social behaviour occurred depending on whether or not animals were part of a settled group and the degree of overlap between animals. Lorises whose home ranges overlapped extensively, slept together

the majority of the time and showed high degrees of cohesiveness, which would be indicative of a gregarious social system as suggested by Nekaris (2000, 2006) for *L. l. lydekkerianus* and exhibited by other prosimians with a unimale-unifemale spatial system: e.g. *Avahi laniger* (Harcourt, 1991) and *Eulemur mongoz* (Curtis and Zaramody, 1998). On the other hand, animals whose home ranges only partly overlapped did not always share the same sleeping site and spent more time foraging on their own, whilst animals that did not share their home range with another animal slept and foraged alone but did have some social interactions with neighbouring animals. These two scenarios would suggest a dispersed social system as observed with other prosimians with a unimale-unifemale spatial system: e.g. *Perodicticus potto edwardsi* in Cameroon (Pimley, 2002), *Nycticebus coucang* (Wiens, 2002), *Phaner furcifer* (Charles-Dominique and Petter, 1980; Schulke and Kappeler, 2002), *Galagoides zanzibaricus* (Harcourt, 1984; Overdorff, 1993), *Lepilemur ruficaudatus* (Zinner *et al.*, 2003) and *Cheirogaleus medius* (Fietz, 1999). One question arises from the fact that some animals shared a sleeping site but did not show high degrees of cohesiveness. Why would they choose to sleep together? One reason would be that it allows them to groom each other and in doing so reduce the number of parasites (Clark, 1985). The solitary female FG had more parasites in her ears and on her neck than any of the other lorises, and spent more time auto-grooming too, thus supporting this hypothesis. The other hypothesis is that a male chooses to share a sleeping site to form a bond with the female and give him an advantage over other males when the female comes in oestrous.

4.2.3.3. Sleeping associations

Loris lydekkerianus lydekkerianus was reported to form multimale-multifemale groups and sleeping groups consisting of multiple males and a single female as occurring frequently (Nekaris, 2006). The significantly larger male home ranges allowed them to have access to more than one female but they were also tolerant of other males. They initiated social interactions with females and provided benefit to females by contributing to parental care (Nekaris, 2006). These findings are slightly different to those of *L. t. tardigradus*. Sleeping groups usually consisted of one adult male and one adult female. In two cases, another individual was part of the group but the sex could not be determined. In both cases though, the other animal appeared younger and/or smaller so they may have been a juvenile, a younger sibling or a subordinate male. Males had slightly smaller home ranges than females and consequently were not able to monopolise more than one female. They did not appear to contribute to parental care as the males of some pair-living primate species do (e.g. *Aotus* and *Callicebus*, Wright, 1990), although male MJ was seen grooming the third individual of the sleeping group, who was smaller and may have been a subadult male. Visits by males (adult and subadult) to younger lorises have been reported in *L. l. lydekkerianus* (Nekaris, 2006). However, lack of observations of parental behaviour renders this point inconclusive. It is highly unlikely that the third individual was an unrelated female as females have shown to be territorial and would gain less from having unrelated females sharing their resources than having an extra male in the group.

It may be that the third individual in one of these sleeping groups was a subordinate male as reported for other slender loris species (Nekaris, 2006). Such a male coalition would occur in the following cases: if the male was a relative, or to help the dominant

male mark the territory of the female, which alone, the dominant male cannot do. In *Galago moholi*, males were reported to sleep with other males. Such sleeping associations usually consisted of an adult and subadult male (Bearder and Martin, 1980) or a mating and non-mating male (Pullen, 2000). In both cases the second male would not be a threat to the dominant male and may thus be tolerated. Females at MPFR have several core areas whereas males only have one. This suggests that a male, whose home range is the same size as that of a female, may need the help of another male to overlap the separate core areas of females. However, even if this other loris was a male, sleeping groups with multiple males and a single female, do not appear to be the norm for *L. t. tardigradus* in MPFR, as reported for *L. l. lydekkerianus*, which may be the result of higher degree of competition for resources.

4.2.4. The mating system

Although behavioural data on mating events are seldom and qualitative in nature, the observed patterns of spatial and social behaviour and data on morphological and reproductive characteristics can give us clues as to the kind of mating system exhibited by lorises at MPFR species (Sterling *et al.*, 2000; Harcourt *et al.*, 1981). So although the spatial and social unimale-unifemale patterns observed would suggest a monogamous mating system (Kappeler, 1997a), other characteristics of the loris behaviour and male reproductive characteristics suggest otherwise:

1. Males had relatively large testes in comparison to other prosimian species. In addition, certain males had larger testes than others. In addition, certain males had larger testes than others (although this could have been related to other factors. See discussion below). These characteristics have been implicated in sperm

competition and typically found in species exhibiting a polygynous mating system (Harcourt *et al.*, 1981; Dixson, 1987).

2. Males that were settled and paired were seen making excursions outside of their 'normal' home range when a female was in oestrous. Similarly, on one occasion when a female was in oestrous, the density of males within the female's home range increased and vocal battles occurred between males.

3. There was some overlap between the home ranges of 'paired' males and those of neighbouring females suggesting the possibility for Extra Pair Copulations (EPCs).

4. Males were significantly heavier than females with a degree of sexual dimorphism of 116 (male weight as a percentage of female weight thus indicating that males were heavier than females).

If lorises at MPFR are not truly monogamous, how could their mating system be described? Based on the four characteristics listed above, the following scenarios are possible, but do not exclude each other:

1. That lorises remain together as a pair for over a year but exhibit a 'flexible' monogamous mating system, whereby males and females have EPCs during times of oestrous (Palombit, 1994; Reichard, 1995; Fietz *et al.*, 2000; Fietz, 2003).

2. That lorises are serially monogamous, unlike primate species exhibiting a long-term unimale-unifemale monogamous system where pairs remain together for more than a year, such as fat-tailed dwarf lemurs (*Cheirogaleus medius*) (Fietz, 1999c) and some sportive lemurs (*Lepilemur* spp.) (Zinner *et al.*, 2003).

3. That lorises are polygynandrous but form two-adult groups for grooming and sleeping advantages (e.g. *Nycticebus coucang*, Wiens, 2002).

4. That lorises exhibit a flexible mating system whereby males compete for females until they have secured a female, at which point, the male and female will have a monogamous mating system as the male maintains a 'best option' scenario with one female. This was observed in *L. l. malabaricus* (Kar Gupta, 2007).

It isn't possible unfortunately to assess the durability of the spatial 'pair bond' as animals were never followed for more than six months. Thus, the first scenario may have been the case at MPFR but no data are available at this stage to verify this. The second scenario proposes that lorises at MPFR formed spatial and social pairs and thus were monogamous but for less than a year. Once again, little data are available to verify this. However, one of the radio-collared females (tracked for a little over six months) was 'paired' with male MD for five months and one day dispersed from her home range. This seemed to coincide with the fact that she had given birth. She eventually settled about 700 metres away from MD's home range near or within the home ranges of male ML and female FM who appeared to form a pair. Could it be that female FB had mated with a male other than MD and upon the birth of her infant, moved out of MD's home range? Similarly, MD, FB's spatial and social partner, was caught within the home range of a neighbouring female, FE. He was caught whilst chasing after FE but after that night, he never ventured into FE's home range again (note that it is unlikely that this male did not return to the catch site as a result of being caught there as all other caught animals returned (sometimes the next night) to where they were caught). However, his sleeping sites, which he shared with FB, were always on the border of FE's home range. This behaviour may suggest the occurrence of EPCs, which have been reported in primate species with a unimale-unifemale

social organisation, including gibbons (*Hylobates* spp.) (Palombit, 1994; Reichard, 1995) and fat-tailed dwarf lemurs (*Cheirogaleus medius*) (Fietz *et al.*, 2000). The African potto (*Perodicticus potto edwardsi*) showed similar ranging patterns in that one male and one female formed a 'social and spatial pair' but genetic analyses revealed that the social partner was not always the male that sired the offspring thus suggesting facultative monogamy (Pimley, 2002).

The relatively high testes volume compared to other strepsirrhines suggests that sperm competition plays an important role in this population as would be expected in species with a polygynandrous mating system (Dixson, 1991, 1995; Harcourt *et al.*, 1995). However, males did not have large home ranges overlapping the home range of several females, as would be expected in a species with a polygynandrous mating system, and as is the case for *L. l. lydekkerianus* (Radakrishna and Singh, 2004; Nekaris, 2000). In addition, in all possible scenarios outlined above, there is the possibility that both males and females engage in EPCs. That females should seek EPCs whilst benefiting at the same time from the advantages of living with a partner should not be ruled out in the case of slender lorises, despite little data currently available, from both studies in the wild or in captivity. Potential benefits to loris females for seeking EPCs would be an increase in genetic diversity of offspring and access to better genes (than those of partner) (Fietz, 2003). A female may have little choice with regards to who she shares her territory with. The benefits provided by having a partner against the costs of being solitary, a female may not have the luxury to be choosy and may have to settle for any partner (Brotherton and Komers, 2003). Thus, EPCs may be used as a female strategy too, which would result in the male's reproductive success decreasing. If that is the case, the large testes and the intra-male variation in size that were recorded in this study may be the product of paired-males

having to frequently inseminate their partner during oestrous to prevent them from getting sired by other males. This would result in testes being larger in order to avoid sperm depletion by frequent copulation (Dixson *et al.*, 1993) without necessarily suggesting a polygamous mating system. Evidence for the occurrence of EPCs in both males and females would require genetic analysis and studies focussing on mate choice and measuring individual reproductive success. The lack of cohesiveness, low levels of association between neighbouring males and females and small number of females present around the male home ranges, would suggest low levels of EPCs. On the other hand, the occasional encounters along home range boundaries may be enough to allow EPCs to occur. Individuals that were part of a pair did not exclusively socialise with their partner, even if the percentage of social interactions with them were significantly higher, and ranging behaviour exhibited by some of the individuals (e.g. FI vocalising whilst walking around the boundary of her territory; or female FF and male MT walking along the boundaries of their home range whilst exchanging calls) may have been indicative of the occurrence of EPCs (e.g. *Hylobates* sp. Palombit, 1994) as opposed to territory defence. In addition, in an area where only two animals were regularly seen, the sudden 'arrival' of more than four males and increase of vocalisations and chases were indicative that the female was in oestrous. For neighbouring males to be aware of this female's reproductive status despite not sharing her home range suggests that the female advertised her status and supports the notion that female lorises may have seeked to mate with other males.

If EPCs do not occur and both males and females show in fact a polygamous mating system, then formations of social and spatial pairs may arise as a result of other advantages, such as grooming and sleeping advantages, as reported for *N. coucang* (Wiens, 2002), and predator defence (Goodman *et al.*, 1993) rather than constitute a

sexual strategy. If this was the case, lorises that formed spatial pairs may not necessarily meet so frequently throughout the night (as opposed to just at the sleeping site for grooming activities). On the other hand, the only animals to show the presence of ectoparasites (lice/fleas) were two of the 'solitary' females (FG and FR) and a male who was solitary when caught (MA). Allogrooming would reduce parasite load and thus provide a net benefit to forming a social pair (Wiens, 2002). Although this alternative explanation for the formation of pairs cannot be ruled out, the data from this study are too few to provide further support. Studies examining more specifically the net benefits (parasite-reducing effect) against the costs of sharing space (higher risk of disease contraction) would be needed. Similarly, despite the presence of predators in MPFR and observations of predation events against lorises by palm-civets, data on benefits of forming sleeping associations with regards to reducing predation rate would need to be collected in order to further test this hypothesis.

The alternative explanation for the larger testes recorded in this loris population along with the 'unimale-unifemale' social and spatial patterns, is that both mating systems (polygamy and monogamy) occur. The male may behave as if in a polygynous mating system but once he has settled with a female he changes his strategy to a more monogamous mating system. This has been proposed by Kar Gupta (2007) and could explain the fact that male lorises have large testes in comparison to other prosimians (because of the element of polygyny) and why some males have larger testes than others within the population (element of sperm competition within a pair-living system as outlined above). In her study, Kar Gupta (2007) showed that males emigrated from their natal home range at a younger age than females, thus resulting in a limited supply of receptive and available females to choose from. As such, once a male attracted a female to his home range, or managed to occupy the home range of a

settled female, she hypothesised that it would become more beneficial for the male to remain with that one female and defend its territory. The same may be true in MPFR since ranging patterns observed are similar to those for *L. l. malabaricus*. However, the lack of data on emigration by males and females renders this point hypothetical and further studies are needed to assess whether emigration differences between males and females are an important factor in social and ranging patterns exhibited by *L. t. tardigradus*.

Furthermore, males of *L. l. malabaricus* (Kar Gupta, 2007) males showed a high degree of intra-sexual competition and those with larger testes also happened to be the healthier males with the settled home range and the female partner, with whom they then remained. These healthier, bigger males were able to monopolise the good habitats, and appeared more attractive to females (Kar Gupta. 2007). Intra-sexual competition based on testis volume and correlations between large testes and social/spatial patterns could not be investigated in this study. However, the large variations in testis size, which occurred between males in this study (ranging between 1084 mm^3 and 3216 mm^3), may not have been related to male status as suggested by Kar Gupta (2007) but other factors. For example, variation in testis size could have been the result of thermoregulation (testis size in *L. l. nordicus* in captivity has been shown to vary significantly with slight changes in temperature (Schulze and Meier, 1995), with testes increasing in volume with an increase in temperature), or the result of seasonal variation, with males caught during the breeding season (if any, see next section) having larger testes than males caught outside the breeding season, as seen in many lemur species (e.g. *Propithecus diademan edwardsi*, Pochron *et al.*, 2002; *Eulemur fulvus rufus*, Ostner *et al.*, 2002; *Microcebus murinus*, Schmidt and Kappeler, 1998). Not enough data were available from this study to test seasonal

variation in testes size in relation to breeding periods or social/spatial status. The two males with the largest testes (~ 3100 mm^3 for MO and 3200 mm^3 for Ma) were caught during potential conception periods (November and March-May). One of these males, MO had a settled home range, which he shared with a female (FI). No data on social and spatial pairing are available for Ma. Male (MT), who was caught just 10 days after Ma, had relatively smaller testes (~2150 mm^3) and was unsettled and unpaired. However, sometime after being caught he was seen settling with a female who came into oestrous sometime in the month of March. On the other hand, male MH, who replaced male MC's position as female FE's 'partner', had testes of approximately 1850 mm^3 when caught at the end of February. Finally, males caught in August, which would fall in between the two conception periods had the smallest testes volume (~1000 - 1700 mm^3). One of these males was unsettled and unpaired whilst another male was settled and appeared to have been paired with a female at some point during the study. These data cannot be used to draw firm conclusions on the mating strategies employed by male lorises at MPFR and the reasons for the observed variations in testes size between males. However, they present an opportunity for new hypotheses to be formulated with regards to the observed variation in testis size between males in lorises and correlates to spatial patterns, reproductive success and body condition.

The mating system exhibited by *L. t. tardigradus* in MPFR cannot be ascertained from this study. What is unlikely however is that *L. t. tardigradus* exhibits a true monogamous mating system. Instead, male and female lorises appear to adopt mixed and complex mating strategies. Studies looking at genetic relatedness in combination with data on spatial and social patterns, reproductive success, as well as

morphological correlates to social/spatial pairing, are necessary to better understand the strategies used by *L. t. tardigradus* to increase reproductive success.

4.2.4.1. Breeding seasonality

The strategies employed by males and females to increase their reproductive success are likely to be influenced by the presence or absence of strict breeding seasonality (e.g. Ridley, 1986; Clutton-Brock and Parker, 1992; Harcourt *et al*, 1995; Mitani *et al*, 1996; Oi, 1996; Nunn, 1999;). Although several studies have looked at the issue of breeding seasonality in both Indian (Rao, 1927; Hill, 1953; Ramaswami and Kumar, 1962; Manley, 1966, 1967; Kadam and Swayamprabha, 1980; Izard and Rasmussen, 1985; Rasmussen and Izard, 1988; Schulze and Meier, 1995; Nekaris, 2000; Kar Gupta and Nash, 2001; Radakrishna and Singh, 2004; Kar Gupta, 2007), and Sri Lankan slender lorises (Osman Hill, 1935; Nicholls, 1939; Nieschalk and Meier, in, Nekaris 2003a, 1984; Goonan, 1993; Schulze *et al.* 1994; Nekaris, 2003a), no consensus as to whether or not slender lorises are seasonal breeders has been reached.

The first study to propose the presence of two oestrous cycles was one by Rao (1927), who observed a conception period in June-July and one in September-November for *L. lydekkerianus* in India. A more recent study on *L. l. lydekkerianus* shows evidence for two oestrus peaks, one in October-December and a smaller one in April-June (Radkarishna and Singh, 2004), whilst a study conducted on *L. l. malabaricus* using radio-telemetry suggests a conception period in November-December and one in April-May (Kar Gupta, 2007). Studies on Sri Lanka lorises have suggested the presence of two breeding seasons (Osman Hill, 1937; Goonan, 1993) but this is based

on lorises kept in captivity and the data are inconclusive with regards to the periods of conception.

Of those that do not support breeding seasonality, Schulze *et al.* (1994) suggest that the long gestation period of approximately six months may give the impression of biannual oestrous cycles when in reality no breeding seasonality occurs (in Nekaris, 2003a). Nekaris (2003a) also does not support the presence of a strict breeding seasonality based on the observations of births throughout the year for *L. l. nordicus* but suggests the possibility of a peak in births during certain times of year (to coincide with periods of greater food abundance) as observed with *L. l. lydekkerianus* (Radakrishna, 2001).

Data collected during this study indicate the possibility that *L. t. tardigradus* shows two breeding seasons. Data on births and the reproductive status of three of the females that were caught indicate a short conception period in November and a longer one in March-May. Changes in the home range size of two females who were in oestrous when caught (in April and in March) suggest that during oestrous females may enlarge their home range. This has been shown to be the case for *L. l. malabaricus*, whereby females actively searched for partners and in doing so, roamed over large areas and vocalised to advertise their presence/reproductive status. Once settled down and paired with a male their home range size decreased (Kar Gupta, 2007). Although data on her reproductive status was not available, female FG showed similar ranging patterns whereby she roamed an area of approximately 15 hectares (calculated using MCP) during the month of February when first caught, and decreased it to seven hectares during the months of March and April, 4.5 hectares in May and eventually, 1.5 hectares in June where she appeared to have settled down (whether she found a male to pair with could not be ascertained). Female FK also

showed similar patterns of home range enlargement, which coincide with one of the potential breeding seasons suggested in this study. She was caught early March and found to be in oestrous. In that month her home range size was approximately 4 hectares and she did not appear to be paired. However, the following month her home range size decreased to 2.7 hectares and in that month she was seen sharing her sleeping sites with male MT, who in the previous months also had been an unpaired (but settled) male. The following months her home range further reduced in size to approximately one and a half to two hectares. The other female who was in oestrous when caught, already was paired and settled with male ML but did not appear to share as large a proportion of her home range with him as other pairs did. In April, when in oestrous, her home range measured 5.7 hectares and a large frequency of calls were uttered (by her and other lorises in her vicinity) suggesting she may have been seeking to mate with neighbouring males, despite being paired. The following months her home range size decreased to 3.8 hectares and one hectare, respectively.

Thus, as demonstrated for *L. l. malabaricus* (Kar Gupta, 2007), this study shows some evidence for home range enlargement by females during times of oestrous and/or when looking to settle and pair up with a male. Unfortunately, data on ranging patterns were limited as a result of a relatively small sample size of animals for each month and the possibility that not all females were reproductively active at some point during the tracking period, making it difficult to draw from these further evidence for breeding seasonality. Nevertheless, for both males and females, an increase in home range size and mean path length were observed during the months of March and April, whilst males showed an increase also in November. Data for the month of November were limited to just one female and thus cannot be used to make any conclusions, even preliminary.

It would therefore seem, based on the evidence gathered in this study, that there is the possibility of two breeding seasons in *L. t. tardigradus*. Whether females are able to come into oestrous twice in the same year cannot be ascertained from the data collected in this study. In addition, studies of slender loris reproduction, both in the wild and captivity, have reported different inter-birth intervals. Intervals of 7.5 and 9.5 months have been reported for *L. l. lydekkerianus* (Radakrishna and Singh, 2004 and Izard and Rasmussen, 1985, respectively), suggesting that females may not be able to have more than one birth a year. On the other hand, Kar Gupta reports three females giving birth in both breeding seasons (November-December and April-May) of that same year. Similarly, slender loris females in captivity (*L. l. nordicus*) have been reported to go into oestrous as early as two days after giving birth and become pregnant during lactation (Schulze and Meier, 1995). More commonly though, oestrus seems to resume six to seven weeks after birth of a surviving infant (Izard and Rasmussen, 1985). Based on this evidence, it is possible that any of the females that were tracked between September 2005 and June 2006 could have been in oestrous at least once during that time. Whether they were in oestrous whilst being tracked cannot be ascertained for most of them though.

To conclude, the data presented in this thesis, together with evidence from the literature suggests that *L. t. tardigradus* may be a seasonal breeder, with two breeding periods occurring at intervals of approximately seven to nine months (and the possibility of a female mating twice in that year). However, Manley (1966) reports that lorisids are poly-oestrous all year round but that in some forms, those that inhabit areas with marked seasonality, two periods of intense breeding occur to coincide with food availability. In her study on *L. l. lydekkerianus*, Radakrishna and Singh (2004) attribute the observed biannual birth peaks to females ensuring that offspring are

weaned just in time for the periods of increased rainfall and presumed food abundance. In her study site, seven months of the year received no rain, whilst one of the wet seasons received less than 100 millimetre per month and the second wet season received between 100 and 300 millimetre per month. No strict seasonality, as is the case in the site in India, occurs in Sri Lanka's Wet Zone. Rainfall data for MPFR was averaged for the years 1998 to 2007 and revealed that the average minimum rainfall was 100mm, and although rainfall patterns appeared to vary greatly from year to year, periods of rainfall of less than 100 millimetre were generally short (less than two consecutive months) and rare. During the radio-tracking study period, only two months had low levels of rainfall, in January and February, and thus, food availability as a result of rainfall patterns cannot be accounted as the main reason for the occurrence of two breeding seasons in MPFR.

The differences in local conditions between habitats occupied by the different slender loris subspecies may explain the discrepancies in the literature about breeding seasonality in slender lorises (Izard and Rasmussen, 1985; Goonan, 1993) and present an opportunity for future research into this topic. The presence of mating seasonality in *L. t. tardigradus* would help explain some of the observed social and spatial patterns. Unfortunately, the data currently available on female reproductive patterns in slender lorises with regards to breeding seasonality, are too few to allow firm conclusions to be drawn as to the influence of mating seasonality on loris mating strategies. Nevertheless I present below some reasons for the observed spatial and social patterns exhibited by lorises at MPFR.

4.2.5. Reasons for observed spatial and social patterns

If lorises are not truly monogamous, then why would they exhibit typically unimale-unifemale social and spatial patterns? Some explanations, not exclusive of each other, can be put forward to explain the observed spatial, social and mating patterns at MPFR.

1. Scarcely distributed and limited resources (food and females)

2. Mate guarding by males

3. Predation risk

1) One of the possible reasons for the observed spatial and social patterns between adult lorises at MPFR is that resources are scarce and/or patchily distributed. Resources may be food or females (Rutberg, 1983; van Schaik and van Hooff, 1983; Wrangham, 1980) and this situation may arise if the sex ratio is male biased as was the case in *Perodicticus potto edwardsi* (Pimley, 2002), or if the ranges of the females are too large for males to monopolise more than one, which would occur in areas where resources are either scarce and/or patchily distributed resulting in females having to have relatively large home ranges (e.g. Woolly lemurs (*Avahi occidentalis*) and fork-marked lemurs (*Phaner furcifer*) (Schulke and Kappeler, 2003, Thalmann, 2001)). Large, evenly distributed and predictable food resources may allow larger group sizes and the possibility of polygyny (e.g. *Loris lydekkerianus lydekkerianus*, Nekaris (2000)). Nekaris (2000) argued that it was the distribution of their main food type (social insects that occur in clumps) that resulted in the observed spatial and social patterns. Pimley (2002) attributed differences in social patterns between the solitary forager *Arctocebus aureus* and the more gregarious *L. l. lydekkerianus* to

differences in the ratio of R (amount of available resources) to N (an individual's needs). Lorises in MPFR fed on social insects but also were observed to feed on flying insects, beetles, caterpillars, geckos and other prey items which, unlike ants and termites, occur singularly or in small groups. In this study I was not able to quantify preferred food type. However, the high density of *Humboldtia laurifolia*, throughout the forest, suggests that in most parts of the forest, the amount of available resources would exceed the needs of the individual, as one tree of this plant species is likely to hold large densities of ants and other insects that lay their eggs within the hollow stems (Krombein *et al.*, 1999). In addition, foraging did not decrease with a decrease in inter-individual distance, suggesting that resource availability was high enough to allow a more gregarious social life amongst lorises at MPFR. However, this may only have been possible because foraging occurred only in the presence of the social partner with which a home range was shared. Resources may not have been plentiful enough to allow more than three animals to adopt a more gregarious mode of life as observed with *L. l. lydekkerianus* (Nekaris and Rasmussen, 2003). Although animals foraged in the presence of conspecifics (within 30 metres), they did not forage as much when they were between five and 10 metres of each other suggesting that their preferred food type may not have been distributed in clumps. Furthermore, the dominance of *H. laurifolia* across MPFR suggests that food distribution is not scarce and is most probably evenly distributed. On the other hand, in section 3.4.1, I have shown that floristic composition in MPFR was fragmented and heterogeneous, which may result in a patchy distribution and availability of insects across the forest, which may explain why females at MPFR had much larger home ranges than female *L. l. lydekkerianus*. In section 5.3.2 I further test this hypothesis by discussing the effect of seasonality (and thus food abundance) on ranging patterns, and show that during the

dry season home range size increases. However, these results must be interpreted with care as they are merely exploratory in nature and based on a relatively small sample size. Nevertheless, it is clear that further investigation of food resource abundance and distribution at fine spatial and temporal scale is needed in MPFR in order to assess the importance of this hypothesis, which cannot at this stage be dismissed.

Scarcely distributed and/or limited resources may be the females. Despite a 1:1 ratio of subadult/adult females and males, the three juveniles that were caught were male, which although is too small a sample size to draw conclusions from, may suggest a male-biased sex ratio in MPFR. A male-biased sex ratio, coupled (possibly) with an uneven distribution of food resources, thus resulting in larger female home ranges, would make it difficult and uneconomical for males to monopolise the home range of more than one female. Males would gain higher reproductive success by maintaining a 'relationship' with one female. This was proposed to be one of the reasons for the formation of pairs in *L. l. malabaricus* (Kar Gupta, pers. comm.) and *P. p. edwardsi* (Pimley, 2002). However, in both cases, there were almost twice as many males as there were females, making this a clear male-biased population. This is not the case in MPFR, making this an inconclusive and unlikely explanation. On the other hand, the operational sex ratio could be male-biased. If females disperse later than males and are thus not easily accessible, then the young dispersing males are more numerous than available females. In addition, not all females may be reproductive during the year. The latter is difficult to evaluate based on data collected in this study but preliminary evidence and evidence from the literature suggest that despite the possibility for two apparent breeding seasons in slender lorises, it's unlikely that female lorises show strict breeding seasonality and it's more likely that most females would be in oestrous at least once a year. However, evidence remains patchy and

more information on the operational sex ratio present in the population and genetics to assess paternity are needed to elucidate whether males opt for the best option scenario (stick to one female both socially and spatially) as a result of limited females (male-biased operational sex ratio).

2) The formation of temporary pair bonds may be a form of mate guarding. One of the assumptions for this hypothesis to be met is that members of a pair spend the majority of their time in proximity and that male competition occurs. One example of a species where mate guarding has been proposed as a reason for the formation of pair-bonds is *Phaner furcifer*, where the male and female of a pair have been reported to spend about 25% of their time in proximity to each other (Schulke and Kappeler, 2003). This is only a slightly higher figure than the figures obtained in this study. In addition, at MPFR males spent the first hour or more at dusk and dawn (and sometimes during the night) grooming the female, suggesting an attempt by the male to strengthen the bond. Allo-grooming only ever occurred between members of a sleeping group and females did not welcome attempts by males outside their sleeping group to socialize with them. However, having not followed a pair for more than six months it is difficult to assess whether these efforts by the male to strengthen the pair-bond, translates into a long-term partnership. The sharing of sleeping sites also may be another form of mate guarding by the male. It is easier for the male to keep track of the female by being there when she wakes up than sleeping somewhere else and having to spend time and energy looking for her during the night. This is especially true as lorises at MPFR regularly changed their sleeping site locations and rarely slept in the same location twice in a row. This may explain why the male, despite venturing away from the female during the night, made sure he returned to the sleeping area before the end of the night.

Another point which adds a question mark to this argument is the fact that FB moved away from MD's settled home range following the birth of her infant. Without having radio-tracked this female for longer, the durability of the bond between her and MD cannot be assessed. She may have temporarily dispersed or simply attempted to increase her home range, and would have eventually returned to MD's home range. The dispersal of a pregnant female from her natal home range was observed in *Galago alleni* (Charles-Dominique, 1977), whilst Pullen (2000) recorded the dispersal of a *Galago moholi* female from her natal home range who later returned. Studies on slender lorises in captivity have shown that conspecifics may react aggressively and potentially injure the newborn (Fitch-Snyder and Schulze, 2001). The alternative is that her infant had been sired by a neighbouring male and she thus left her home range to avoid retaliation by MD, her social partner.

The fact that FE's first partner, MC disappeared and was quickly replaced by male MH suggests that paired males may benefit from year-round mate-guarding. Their absence may be sensed by neighbouring males as a result of the sudden lack of scent-marks deposited by the previous partner to cover up the female's 'advertising' scents (Brotherton, 1994, in Brotherton and Komers, 2003)). Attempting to save more than one territory and thus leave room for other males to take over unguarded territories would result in the male losing that territory and access to that female. Mate-guarding a female may thus provide the males in MPFR with more benefits than costs, especially if EPCs occur with neighbouring females.

From the female's point of view, she may be more receptive to a male who has been her social partner and helped her defend her resources, than a visiting male. It has been shown in studies on pygmy lorises (*Nycticebus pygmaeus*) that a male that has been the spatial and social partner of a female for a period of at least 30 days prior to

oestrous, resulted in higher number of offspring than pairs that did not spend time together prior to the female coming into oestrous (Fitch-Snyder and Jurke, 2003). Females at MPFR were seen fending off unwanted male suitors, in some cases reacting aggressively by physically pushing the male away, whilst uttering repetitive chitter calls. This only occurred between neighbouring males and females. A female also would gain from associating with one male who would help with infant survival, either directly or indirectly, by either helping females defend their resources, or protecting it from infanticide (van Schaik and Dunbar, 1990), or predators (Dunbar and Dunbar, 1980)

3) It is thought that solitary individuals are more vulnerable to predation. As a result group living, both at the sleeping site as well as in the night, is viewed as an adaptation to reduce predation risk (Isbell, 1994), through active group defense, increased vigilance and dilution (Kays and Gittleman, 2001). However, this may not hold true for the more cryptic nocturnal primates. Predators were abundant in MPFR and chases by palm-civets were observed on two accounts. I showed that activity decreased when the moon was bright during the dry months, when visibility is increased as a result of decreased foliage. This may suggest that predation is perceived as a risk by lorises and that the cost for males of having to defend a large home range outweighs the reproductive benefits (Kays and Gittleman, 2001; Stanford, 2002). This explanation may be backed up by the fact that in an area devoid of predators, *L. l. lydekkerianus* exhibited a multimale-multifemale spatial system, whereas in KMTR where predators were present, *L. l. malabaricus* exhibited a spatial system similar to that seen in this study (Kar Gupta, 2007). As mentioned in the previous point of this section, females would benefit from associating with a male, who would help defend them against predators. On the other hand, the female FB

dispersing from her home range with a newborn renders this point inconclusive as predation risk would have been high for both the female and the infant and the benefits of dispersing, or the costs of staying, must have thus been much higher than the potential risk of predation during dispersal.

4.2.6. Conclusion

The social organisation of *Loris tardigradus tardigradus* is complex. Males and females appear to have a unimale-unifemale spatial system, with a social system ranging between dispersed and gregarious depending on the spatial interactions animals have. *L. t. tardigradus* differs from *Loris lydekkerianus lydekkerianus* in the spatial system but is similar in having a high frequency of social interactions. Similarly to *Loris lydekkerianus malabaricus*, *L. t. tardigradus* has a unimale-unifemale spatial system and little intra-sexual overlap. Without data spanning more than one year, genetic analyses to test paternity, and direct observation of mating events between radio-collared animals, the mating system exhibited by *L. t. tardigradus* at this stage cannot be ascertained. However, there is enough evidence to suggest that *L. t. tardigradus* is not a true monogamous species but rather forms spatial and social pairs, with either a serial monogamy mating system or a long-term pair-bond with the occurrence of EPCs as has been reported in primates with a unimale-unifemale social system (e.g. *Cheirogaleus medius*; Fietz *et al.*, 2000) or a more flexible mating system as has been suggested for *L. l. malabaricus* by Kar Gupta (2000). More long-term studies on this population as well as others in habitats with differing ecological pressures are vital if we are to elucidate the social organisation and degree of complexity exhibited by this species.

4.3. ECOLOGICAL PLASTICITY OF *L. T. TARDIGRADUS*

The second aim of this thesis was to investigate the degree of ecological plasticity exhibited by *Loris tardigradus tardigradus* in relation to habitat and microhabitat needs, and in relation to seasonality and moon phase. Do lorises choose specific habitat and microhabitat features or are they able to make use of available habitat? Do lorises change their activity and ranging patterns in relation to seasonality (rainfall and temperature) and moon phase? These are the questions I aimed to answer in this thesis and will discuss in this chapter.

4.3.1. Plasticity at the habitat level

L. t. tardigradus showed preference for forest habitat rather than agricultural land, actively managed plantations or home gardens, which they completely avoided, unlike other loris taxa, which appeared to prefer plantations (Wiens, 1995) or open scrubland (Nekaris, 2001). Within MPFR, habitat partitioning occurred with one area having higher species richness, lower tree density and dominance by *Dipterocarpus zeylanicus*, a canopy species commonly found in undisturbed lowland rainforest. Nocturnal surveys through these areas did not yield any loris sightings, whereas areas that were more disturbed, and were characterised by, lower species richness, higher tree density and dominance of the late-successional understorey tree species *Humboldtia laurifolia* and the bamboo shrub species *Ochlandra stridula*, and thus more disturbed (Ashton *et al.*, 2001) appeared to hold a higher density of slender lorises.

The absence of sightings does not equate to the absence of lorises but at best would suggest that slender loris density in the less disturbed areas was particularly low.

Thus, it seems that slender lorises at MPFR prefer disturbed or semi-degraded areas. The patchy distribution of lorises at MPFR had previously been noted during short-term surveys (Nekaris *et al.*, 2005) but since surveys were conducted over a shorter period of time (although adding up to four months of study over time) and without the use of radio-tracking, a relatively smaller area was covered during surveys. Vegetation surveys also were limited to a relatively smaller area, which happened to be dominated by *H. laurifolia*, a species typically found in disturbed areas. Thus, results may have been biased and clarification and confirmation was necessary. In this study, the use of radio-tracking allowed a wider extent of the forest to be surveyed and sampled. The discovery of areas with lower disturbance level and the correlated lower density of lorises reinforce the idea that slender lorises may prefer disturbed or semi-degraded habitats to undisturbed habitats.

The area of low loris density may have been unsuitable in terms of either: resource quality and/or quantity, predation risk, and/or vegetation structure. Without systematic insect surveys conducted over a period of a year in areas of differing loris abundance, the first possibility cannot be discussed. Resources are undoubtedly an important factor determining the distribution of females, and hence males, as supported by the observed increase in home range size during the dry season. However, it is highly unlikely that lorises did not use this area, as a result of the relatively lower resources found within it. Instead it is most probably a combination of the latter two points (predation risk and vegetation structure). The fact that there is less undergrowth and more tall trees in that area suggests that it is more difficult for lorises to move around in that area (Ganzhorn, 1993) and to avoid predators (Stanford, 2002) . The larger gaps between trees as a result of lack of lianas and vines and undergrowth and smaller trees would result in higher energetic demands for travelling. Although systematic

surveys of predator abundance in either area were not conducted, sightings of potential predators were more frequent in the undisturbed area than other areas. Thus, increased predation risk together with increased energetic demand for travelling, would render this area less suitable for lorises. Additionally, the lack of undergrowth and tangled vegetation makes hiding and escaping more difficult. Observation of a radio-collared loris being chased by a golden palm-civet revealed that palm-civets have a lot of difficulty travelling on small-sized lianas and vines, giving the 150-200 gram loris a distinct advantage. In areas devoid of such structures lorises would not be able to escape the large carnivore as easily. Additionally, data on sleeping sites revealed that lorises use tangles of lianas, vines and/or small branches between trees more than expected. This, again, is probably to reduce risk of being caught by predators.

Indeed, Nekaris *et al.* (2005) identified this as being one of the main reasons for the high density of lorises found at MPFR, compared to other forest patches. However, without conducting vegetation surveys in other forest patches, which may have a similar floristic composition to MPFR, it is difficult to attribute the high loris density observed at MPFR to this factor alone. Instead, it may be that MPFR provides a multitude of factors that together constitute a suitable environment for lorises. A recent study by Nekaris (unpublished data) which re-analysed data from surveys conducted in nine forest patches, including MPFR, forest patch size was identified as being the only factor strongly correlated to slender loris abundance. When the effect of fragment size was removed, a negative relationship was found between slender loris abundance and number of lianas. The abundance and biomass of lianas is typically positively associated with disturbed and fragmented forests (Laurance *et al.* 2001). Vegetation surveys revealed that the presence of lianas in the study site was

occasional. This is similar to the findings from Nekaris' study (Nekaris, unpublished data) where an average of 0.8 ± 1.2 lianas (per tree surveyed) were recorded. Other forest patches with higher human disturbance levels had an average of 2.4 ± 1.6 lianas per tree surveyed.

4.3.2. Plasticity at the microhabitat level

4.3.2.1. Substrate use

Slender lorises used small substrates more than medium or large substrates. Although, substrate size availability was not measured, areas used by lorises were highly disturbed and dominated by *Humboldtia laurifolia* and *Ochlandra stridula* both of which lack medium and large branches. This would suggest that small-sized substrates would be more available than large-sized substrates in those areas. A study on *L. t. tardigradus* at MPFR measured the availability of substrates of different size at a height of three and half metres, which was identified as the average height used by lorises. Substrates of less than 10 centimetres accounted for 88% and thus it would appear based on this that lorises use what's most commonly available. However, these vegetation surveys were conducted in areas dominated by *H. laurifolia* and where small-sized branches would thus be more common than larger branches. Areas such as SS1 had a relatively high abundance of large trees with large-sized substrates, suggesting that preference for small substrates may indeed exist and could be a result of morphological constraints and behavioural adaptation to reducing predation rate. The small-sized hands and feet may prevent them from easily moving on large substrates whilst their small weight would allow them to move on small substrates. The preferred use of smaller substrates may also be a behavioural adaptation to reduce predation rate (Stanford, 2002). Using smaller-sized substrates would reduce their risk

of being caught by palm-civets, due to the inability of the latter to move on small substrates.

Although lorises used smaller-sized substrates more frequently, they were also observed using the larger-sized substrates such as trunks and large branches but at lower frequencies, as reported during previous surveys (Nekaris and Jayewardene, 2004; Nekaris and Stevens, 2007). Walking on large branches did not appear to slow them down but climbing up and down large trunks appeared less effective as a form of locomotion. Although this is based solely on observations of the speed at which they moved on such substrates, there is evidence from studies conducted in captivity and looking at grasping ability of lorises and locomotor velocity, that walking on such substrates is less effective as a result of the hand and foot span being too small to effectively grasp the substrate (Schmitt and Lemelin, 2004; Schmidt and Leuchtweis, 2007; Kirk *et al.* 2008; Stevens, 2008), thus potentially putting them in a vulnerable position.

These patterns of substrate use are similar to those observed in *L. l. lydekkerianus* (Nekaris, 2000) in that small substrates were favoured over medium and large ones. However, some differences exist, which may be reflective of differences in forest characteristics between the two sites. The study site in India consisted mainly of thorny bushes, short trees and scrubby undergrowth (Nekaris, 2000), whereas at MPFR, taller and larger trees were more frequent. Thus, the lower frequency of use of larger substrates by *L. l. lydekkerianus* in comparison to *L. t. tardigradus* appears to reflect substrate availability rather than inter-specific differences in microhabitat preference.

Unlike tarsiers and bushbabies whose locomotor behaviour is typified by clinging onto and leaping off vertical supports (Cartmill, 1974, Charles-Dominique, 1977), lorises, despite also having rapid locomotion, are quadrupedal arboreal climbers whose morphology is more specialised to bridging gaps and walking along a continuous plane (Charles-Dominique, 1977; Bearder, 1987; Barrett, 1984; Nekaris, 2000). Thus it is not surprising to find that lorises at MPFR used horizontal and oblique substrates more often than vertical substrates. Nevertheless, the use of vertical supports was relatively high (18% of total observations) and this is mostly as a result of lorises using the trunks of bamboo plants, whilst foraging. This plant forms thick bushes and lorises were able to bridge between vertical trunks quite easily, whilst reducing predation risk by being camouflaged within the thick bamboo bush.

4.3.2.2. Plant species

Just as the use of saltatory locomotion reduces predation risk for tarsiers and bushbabies (Crompton and Sellers, 2007), the use of camouflaged vegetation such as bamboo may be a way to reduce exposure to predators (Longland and Price, 1991). This may be one of the explanations for the preferred use of this plant species. Based on vegetation surveys though, bamboo was a dominant shrub species in MPFR and thus the frequency of use observed may simply reflect the availability of this plant species. In addition, lorises always responded to predator presence by climbing up rather than down. Being in a low bush, no matter how dense, may pose too much of a risk once spotted.

The frequency of use of bamboo (e.g. *Ochlandra stridula*) and other bushes for foraging would thus suggest that the benefits gained from feeding from these plant species, are greater than the risks posed by foraging at low levels (Brown, 1999) and

may reflect the fact that they are hosts to a high abundance of insects. This may indeed be the case, as bamboo was predominantly used for foraging, and grooming, which often occurred after a feeding bout. Surveys of insects on bamboo were not conducted but *ad libitum* observations of insects present on bamboo bushes revealed the presence of wood-chewing beetles (*Chlorophorus annularis*: bamboo borers). The latter use the water-tight internodes of bamboo branches to lay their eggs (Haojie *et al.*, 1998). Once hatched, the beetles chew their way out, leaving behind a bigger hole which fills with water. These are known as phytotelmatas (plant-held water habitat), and are small ecosystems in themselves in which both water and insects, particularly diptera, can be found (Maguire, 1971). In addition to foraging in bamboo, lorises were observed sucking on one of these small bamboo branches, presumably for water. The loris would grab the small branch with both hands and either lick the inside of the branch or suck on it. The presence of a high density of arthropods in bamboo habitat has been documented in a study conducted in lowland rainforests in Peru (Pearson and Derr, 1986). The phytotelmatas present in bamboo may thus also act as drinking sources, which also happen to be filled with insect larvae. A similar situation was described for *Loris lydekkerianus lydekkerianus* whereby lorises ate the pods of *Prosophis chilensis* possibly because of its water content (Greegor, 1980, in Nekaris and Rasmussen, 2003). The presence of both water and the high density of arthropods, would make bamboo a resource important enough to lorises to outweigh the risks of being on lower grounds whilst foraging.

The other plant species used frequently by lorises at MPFR was *Humboldtia laurifolia*. Like *Ochlandra stridula*, this plant species was frequent in most areas of the forest and thus frequency of use may simply reflect availability. However, like bamboo, this plant may have also provided some benefits to lorises, either structural

and/or as a source of food. The hollow stems of *H. laurifolia*, known as intermodal domatia, are packed with insects, particularly ants, of which fourteen different taxa have been identified (Krombein and Norden, 1997, Krombein *et al.* 1999). A study by Nekaris (Nekaris and Rasmussen, 2003, Nekaris and Jayewardene, 2003) identified ants as being the preferred insect to lorises, which would make this plant species a valuable and reliable source of food for lorises. Unlike bamboo, this plant species makes up a safer microhabitat to lorises on which to rest, sleep and groom, without fear of being caught should they be spotted by a predator. Predators such as civets, palm-civets and fishing cats have often been seen resting on the thick branches of *H. laurifolia*. However, they cannot easily move around the smaller and tangled branches of this plant species, giving the loris a clear advantage. Thus, *H. laurifolia* constitutes for the slender loris a perfect microhabitat for both foraging and safety. It is not surprising therefore that this plant species was so frequently used independent of the fact that it was the most dominant species around MPFR.

4.3.2.3. Inter-sexual differences in microhabitat use

In this study I have shown that males and females at MPFR formed 'spatial pairs', and in most pairs, shared much of the same area. This may explain the lack of significant differences found in the way males and females used their microhabitat. On the other hand, differences in microhabitat use between members sharing a home range (as a form of resource/niche partitioning) may have been diluted by patterns of microhabitat use exhibited by individuals not sharing their home range with others, and differences (although not significant) seen between males and females may be worth investigating in further studies to assess whether males and females sharing a home range minimise competition for resources through resource and/or spatial

(vertical) partitioning. For example, although no significant differences in height use were shown and inter-individual variation was high, median values for heights above six metres were higher for males than for females. Other inter-sexual differences, although not significant but worth mentioning, include the differential use of three of the most dominant species, *H. laurifolia*, *O. stridula* and *D. retusa*, whereby males used *D. retusa* more frequently than *H. laurifolia* and *O. stridula* and females used the latter two species more frequently than *D. retusa*. Inter-sexual resource or niche partitioning has been documented mainly in birds, particularly woodpeckers (Picidae family) (Williams, 1980) and woodhoopoes (Phoeniculidae family) (Radford and Du Plessis, 2003), but has been less well documented in mammals, except for the sexual discrimination of habitat use in *Peromyscus* and *Microtus*, which Morris (1984) suggested may have been a way to reduce inter-sexual resource overlap. The apparent preferential use by females of *H. laurifolia* and *O. stridula* in comparison to males may reflect differences in reproductive constraints (McNab, 1984; Izard and Rasmussen, 1985). These two plant species, who act as hosts to insects, constitute reliable and easily locatable sources of food for females (Morris, 1984) so although males, like females, used these two dominant plant species frequently, they used *D. retusa* more frequently than either *H. laurifolia* or *O. stridula*, suggesting some difference in preferred plant species between sexes. The lack of significance may have been the result of pooling individuals that shared home ranges with one or more individuals and those individuals that were 'solitary'. Further investigation of differences between members of a group, comparing animals sharing their territories and solitary animals, with regards to microhabitat use would be necessary to better understand the role of microhabitat and resource partitioning within a population and how this may be affected by ranging patterns.

Other inter-sexual differences, although not significant, include the use of three of the most dominant species, *H. laurifolia*, *O. stridula* and *D. retusa*, whereby males used *D. retusa* more frequently than *H. laurifolia* and *O. stridula* and females used the latter two species more frequently than *D. retusa*. Inter-sexual resource or niche partitioning has been documented mainly in birds, particularly woodpeckers (Picidae family) (Williams, 1980) and woodhoopoes (Phoeniculidae family) (Radford and Du Plessis, 2003), but has been less well documented in mammals, except for the sexual discrimination of habitat use in *Peromyscus* and *Microtus*, which Morris (1984) suggested may have been a way to reduce inter-sexual resource overlap. The apparent preferential use by females of *H. laurifolia* and *O. stridula* in comparison to males may reflect differences in reproductive constraints (McNab, 1984; Izard and Rasmussen, 1985). These two plant species, who act as hosts to insects, constitute reliable and easily locatable sources of food for females (Morris, 1984) so although males, like females, used these two dominant plant species more frequently than most other plant species within MPFR, they used *D. retusa* more frequently than either *H. laurifolia* or *O. stridula*, suggesting some difference in preferred plant species between sexes. Further investigation of differences between members of a group, comparing animals sharing their territories and solitary animals, with regards to microhabitat use is necessary to better understand the role of microhabitat and resource partitioning within a population and how this may be affected by ranging patterns.

4.3.3. Effect of abiotic factors

4.3.3.1. On activity

When activity scores were tested against three variables, temperature, rainfall and NII, during the months between August 2005 and June 2006, temperature was the only factor that showed a near significant effect on activity, which decreased with a decrease in temperature. This may be explained by the following:

1. To save energy at a time of year when months are on average drier, resulting in lower foliage biomass and possibly decreased abundance and or diversity of arthropods.

2. To reduce predation risk at a time when, with reduced foliage, visibility is increased and presumably predator exposure is higher.

1) Several studies have provided evidence showing that insects in the tropics undergo seasonal changes in abundance where dry and wet seasons alternate (Buskirk and Buskirk, 1976; Wolda, 1979a). This is the case in areas where the dry season is pronounced as well as areas where it is rather mild. In both cases, insect abundance decreases (Fogden, 1972). On the other hand, a study conducted in Costa Rica found that insect abundance increased during the mild dry season in secondary vegetation (Janzen, 1973). More recent studies studying the effect of rainfall on specific insect orders or genera, demonstrate the complexity of this relationship (e.g. Intachat *et al.*, 2001; Hill *et al.*, 2003) and as a result, general predictions of insect abundance during different times of the year cannot be made without backup data based on thorough, systematic and long-term insect surveys. This obviously would be time-consuming and for the purpose of a study looking at slender loris food abundance and

distribution, a detailed analysis of preferred insect orders (and ideally species) by lorises and the seasonal changes in abundance of these insect orders would be necessary to test this idea. Despite the decrease in overall activity, there was an increase in home range size during these drier months, which is possibly indicative of a decrease in resource quantity, resulting in lorises having to expand their home range to meet their metabolic requirements. A decrease in foliage was certainly observed during the months of January and February when slender loris activity decreased. In a forest that is small and where territoriality between females is high, slowing down activity thus reducing energy loss, may be the best way to cope with a decrease in food availability.

2) The second explanation for reduced activity during the months of December to March is predation risk. During these months foliage greatly reduces in biomass and visibility is increased as a result. This was also noted during a previous study at MPFR (Nekaris, pers. comm.). Predation risk would presumably increase with visibility as the main predators of lorises at MPFR (civets and owls) rely primarily on vision to detect their prey. On the other hand, lorises would also be able to spot predators better and thus escape sooner.

When activity was analysed against NII no significant effect was observed. However, when the effect of luminosity on activity was tested during the colder and drier months only, NII contributed significantly towards the variance in activity scores and the relationship between the two variables was negative, suggesting that as NII increased, activity decreased. It could be that during months when foliage is reduced and the detection potential for predators increased, lorises are more exposed and vulnerable to predatory attacks. It has been shown that for some prosimians increased luminosity provides an advantage, not only because the animal is able to spot the

predator and thus escape a potential attack, but also because some predators hunt better in the dark (Bearder *et al.*, 2002). Thus, studies on the effect of luminosity on successful predatory attacks by loris predators are necessary in order to better understand how luminosity affects loris anti-predatory behaviour.

Interestingly, in an area devoid of predators, *L. l. lydekkerianus* increased time being inactive and decreased time exploring as moonlight increased but no differences were noted on locomotion or feeding (Radakrishna and Singh, 2002). However, another study, conducted on the same population, reports almost contradictory results, with foraging and travelling between trees increasing with increasing luminosity (Bearder *et al.*, 2002), whilst other behaviours such as feeding and exploring, did not show any change. In this study, no difference was found between dark nights and bright nights with regards to either foraging or travelling. Instead, grooming and sleeping/resting were much more frequent during bright nights. This may simply be as a result of the observers having a higher chance of spotting the animals exhibiting behaviours that are normally difficult to observe, as a result of the brighter conditions.

These results demonstrate the difficulty in assessing the effect of moonlight (and other abiotic factors). Abiotic and biotic factors are interlinked to varying extents, and the activity budget exhibited by individuals of a population, will be the result of a combination of the effect of each of these factors, such as temperature, luminosity, rainfall, predator risk, food availability, etc. Although the results presented in this thesis do not entirely elucidate the effect of abiotic factors on loris behaviour, they nevertheless present an opportunity for new hypotheses to be formulated for further testing with regards to the main environmental pressures that affect their behaviour (Predation risk? Resource distribution and abundance?) and the extent to which they can adapt to changes in the environment.

4.3.3.2. On ranging patterns

A negative correlation was found between home range size and rainfall indicating that during the dry months lorises responded by increasing their home range. Although changes in home range size may be affected by factors such as dispersal, reproductive status (whether a female is pregnant, in oestrous or lactating) or breeding season (e.g. Chaverri *et al.*, 2007), it is also possible that the observed increase in home range size is related to a reduction of resources or water during the drier months of the year. Although it is known that female home range size is mainly determined by the occurrence and distribution of resources (Emlen and Oring, 1977; Harvey and Clutton-Brock, 1981), changes in home range size as a result of seasonality are expected in primates inhabiting habitats with strong seasonality such as the dry deciduous forests of western Madagascar (Dammhahn and Kappeler, 2005). MPFR did not show this level of seasonality and thus a change in home range size as a result of a relatively short dry period is unexpected but shows a potential species-specific behavioural strategy to survive times of low resource availability. Additionally, although MPFR is not a deciduous forest, it is semi-evergreen and exhibits a typical cycle of reduced foliage biomass before the next growing season. Although not systematically and quantitatively measured, we noticed in both 2005 and 2006, a clear reduction of foliage and drying out of leaves during the months of January and February (starting in December and extending until March). These times also coincide with villagers going into the forest to collect firewood, as accessibility and visibility inside the forest is increased. A reduction in foliage biomass would no doubt have an effect on insect abundance, distribution and quality, as well as water availability.

Such changes in home range size as a result of changes in seasonality have not been documented in other studies on slender lorises. Instead, Kar Gupta (2007) reports

changes in the frequency of use of different forest types according to rainfall, with lorises using dry deciduous and scrub forests less than riverine and evergreen forests during the dry period. It remains to be investigated though whether lorises may have altered the frequency with which they used certain habitat types (edge, interior forest) in response to seasonal changes. Food availability also was not measured systematically across different parts of MPFR and at different times of the year Such studies would shed light on observed changes in home range size during certain periods of the year, particularly in a forest where seasonality does not follow a predictable pattern.

4.4. CONSERVATION IMPLICATIONS AND PROPOSALS

4.4.1. Conservation implications of this study

The rising movement toward integrating the fields of animal behaviour and conservation biology over the last decade is apparent in the recently published books 'Animal Behavior and Wildlife Conservation' (Festa-Bianchet and Apollonio, 2003); 'Behaviour and Conservation' (Gosling and Sutherland, 2000); 'Behavioral Ecology and Conservation Biology' (Caro, 1998); and 'Behavioral Approaches to Conservation in the Wild' (Clemmons and Buchholz, 1997) and articles (e.g. Reed and Dobson, 1993; Ulfstrand, 1996; Sutherland, 1998; Caro, 1999; Caro, 2007) all of which promote the value of combining behavioural ecology with wildlife conservation and management. *Loris tardigradus tardigradus* is currently classified by the IUCN as Endangered (C2A(i)) but currently no conservation actions have been taken towards reducing the threats of extinction that this species faces, although conservation plans have been put forward by the EDGE programme run by the

Zoological Society of London. The first step in planning conservation strategies for a species is to collect baseline data on its behaviour. Knowledge of individuals' behaviour has the potential to alter the understanding of how populations fare in fragmented habitats, the responses of populations to exploitation and disturbance, disease susceptibility, effective population size, captive breeding and reintroduction efforts, and population monitoring and modelling (Caro, 1999). Although much work has been conducted on wild populations of *L. t. tardigradus* (Phillips, 1935; Hladik and Petter, 1970; Petter and Hladik, 1970; Nekaris *et al.* 2005, Nekaris and Jayewardene, 2003), neither the social organisation nor the degree of plasticity exhibited by this species were studied. In addition, the structure of any of the populations of *L. t. tardigradus* dispersed throughout the Wet Zone never have been studied, resulting in a lack of estimates of sex ratios or number of mature individuals in different forest patches. Thus, the third aim of my thesis was to use the information collected on population structure and social organisation and behavioural ecology of *L. t. tardigradus* as a stepping stone for conservation plans for this endangered species. I organise this chapter by presenting conservation goals for *L. t. tardigradus* and for each of these goals reveal the implications and use of this thesis' findings and propose avenues for future research to meet these goals.

1. Improving baseline information

Prior to this study relatively little was known of the behaviour of *L. t. tardigradus*. This is not only as a result of the lack of studies conducted in the wild but also as a result of *Loris tardigradus* being the rarer of the two in captivity (in comparison to *L. lydekkerianus*), thus leaving little opportunity to study it. Without the knowledge, acquired from baseline behavioural data, of what constitutes normal, adaptive

behaviour in the wild, comparisons across time and space cannot be made and changes (environmental and anthropogenic) cannot be understood (Clemmons and Buchholz, 1997). With this long-term study I provide some data for comparison so that a better understanding of the way individuals adapt to changes and their impact can be gained. Studies on *Loris lydekkerianus lydekkerianus* proposed canopy continuity as a predicting factor for slender loris density (Singh *et al.*, 2000; Kumara *et al.*, 2004) and Nekaris (pers.comm.) suggested that for *L. t. tardigradus* the most defining factor of population density may be forest patch size (positive correlation) and vine density (negative correlation). Although studies looking at ecological correlates to population density can be invaluable in predicting distribution across a wide area, such associative approaches to conservation do not account for time, and thus fail to identify the conditions necessary to ensure that species persist over time (Boyce *et al.*, 2007).

The need to evaluate the impact of the environment on species persistence through time can only be met by collecting baseline data over a significant span of time, which can then be used to estimate the likelihood of a species surviving in a particular habitat. However, using the same methods of evaluating density or abundance and conducting surveys in a systematic manner also are crucial for this purpose. This study is a perfect example. Nekaris and Jayewardene (2004) reported a slender loris encounter rate in MPFR of 13 animals per kilometre in 2001, and 1.1 animals per kilometre in 2004. This study revealed an encounter rate of 0.70 animals per kilometre across the entire area of MPFR, and an abundance estimate of 1.06 animals per kilometre across the area surveyed in previous years (Nekaris and Jayewardene, 2004). Although it may well be that the slender loris population decreased between 2001 and 2005 (based on reduction in reported encounter rates between the study in

2001 and earlier studies), it seems unlikely that it would have decreased so dramatically. Although the extent of MPFR reduced between 1968 and 1986 and was further reduced since then with the plantation of pine forest plantations, it is unlikely that the extent of the forest has dramatically changed between 2001 and 2005 and unlikely to be the reason for such disparate reports of encounter rate. It seems more likely that differences in methodological aspects may have resulted in different reports. In surveys conducted in 2001, less than 20 kilometres were walked and surveys were restricted to the area SA1, reported in this study as having the largest number of lorises compared to other areas in MPFR. The encounter rate calculated for that area is nearly the same as that reported by Nekaris and Jayewardene (2004) for the year 2004. It is thus vital for comparative purposes, that surveys be done systematically and that methodological aspects remain the same, so that factors affecting slender loris abundance/density may be evaluated and the way the species responds to further change, predicted.

Monitoring and managing species are central issues to conservation and bioacoustics research and tools can provide insights into animal behaviour, which in turn can aid conservation efforts (Baptista and Gaunt, 1997). In this study I describe the vocal repertoire and behaviour of *L. t. tardigradus*, who differs from *L. lydekkerianus* in a number of ways. In India, Nekaris (2000) reported *L. l. lydekkeranus* as calling at a rate of 3.5 to 5.4 times per hour unlike *L. t. tardigradus* who called at a rate of approximately one call per hour. In addition, *L. t. tardigradus* called more frequently at the beginning of the night, unlike *L. l. lydekkerianus* who called equally frequently at all times of the night. In a preliminary study looking at bioacoustic differences between *L. L. nordicus* and *L. t. tardigradus* in Sri Lanka, Coultas (2002) revealed some differences between the two species. *L. t. tardigradus* uttered more multiple-

tone whistles (91.7 %) than *L. l. nordicus* (43.8 %) and uttered a whistle type (referred to as call type 5 in Coultas (2002)) that was highly modulated and contained the greatest number of harmonics and broadest frequency bands than whistles recorded for *L. l. nordicus*. Differences reported between this study and those on *L. l. lydekkerianus* may be the result of environmental features, characteristic of different forest types, but they may also reflect taxonomic differences (Zimmerman *et al.*, 1988; Martin, 1990; Honess, 1996). Despite the taxonomic status of slender loris taxa in Sri Lanka having been confirmed through morphological studies (Groves, 1998, 2001), behavioural studies (Nekaris and Jayewardene, 2003, 2004) and phylogenetic studies of museum specimens (Nekaris *et al.* 2006), additional data on bioacoustics would be invaluable in confirming the current status of sender loris taxa in Sri Lanka.

Monitoring the acoustic environment is particularly useful in environments such as tropical rainforest where accessibility and visibility are low, particularly when the species in question is difficult to observe (Baptista and Gaunt, 1997). In this thesis I describe the frequency at which different call types were heard and the context in which these calls were heard (between pairs, between mother and infant, etc.), which may complement otherwise minimal data based on visual surveys alone. Needless to say, the data collected in this study are in many ways preliminary and future comparative studies are needed to better understand the acoustic behaviour of lorises and allow such data to be used more efficiently. However, behavioural data, particularly in the absence of genetic analyses, is vital in showing species-specific characteristics and helping conservation efforts.

2. Improving population models

This brings me onto my next conservation goal. As I briefly presented in the previous section, past studies on slender lorises have quantified slender loris presence and abundance (or density) and the habitat characteristics of their localities to isolate environmental components that can identify where slender loris species are found. Although this information is necessary to identify critical habitats for a species (Scott *et al.*, 1993), the knowledge gained from process-based approaches (such as PVA and meta-population analysis) can predict distribution, abundance and population dynamics and thus, extinction risk of populations (Johnson, 1994; Akcakaya *et al.* 2007). Whether associative or process-based models are used, the process of modelling would result in (at the least) a set of hypotheses that can then be evaluated and tested (Dunbar, 2002), and in doing so, reveal the underlying biology of the species and help to manage conservation efforts more effectively, both in the wild and in captivity. This is vital in a situation where there is little time and room for error, such as the conservation of an endangered primate. The mating system of a species will have a great influence on the number of individuals that will contribute offspring to the next generation (*Ne*) (Cowlishaw and Dunbar, 2000). Mate choice (generally by females) and mating system directly influence *Ne* by their effect on breeding sex ratio and on distribution of reproduction (Anthony and Blumstein, 2000; Sutherland and Norris, 2002). Thus, *Ne* in monogamous species will constitute of more or less the same number of breeding adults, unlike species with a polygamous mating system, where only some males will contribute offspring to the next generation, thus showing a reproductive skew. For that reason, polygynous species are thought to typically show a low *Ne* and hence such species are expected to be more vulnerable to genetic stochasticity than monogamous species (Dobson and Lyles, 1989). However, in

certain situations, monogamous species should be more, not less, susceptible to extinction than polygynous species because the death of a single individual may mean that its mate does not reproduce (Legendre *et al.*, 1999).

The mating system of *L. t. tardigradus* in MPFR could not be ascertained. Spatially and socially lorises formed pairs. However, it is unlikely that their mating system was truly monogamous. At the time of oestrous males other than the paired male attempted to mate with the female, but females seemed more likely to reject an unpaired male than either the male with whom she shared her home range or a neighbouring male with a stable home range. If this is the case, as seen with *L. l. malabaricus*, variance in male reproductive success will increase and consequently decrease *Ne*. While calculating *Ne*, EPCs should be taken into account, as in theory, they could either increase or decrease variance in reproductive success among males (Parker and Waite, 1997; Webster *et al.*, 1995). Brashares (2003) found that monogamous and mildly polygynous West African mammals were more prone to extinction than highly polygynous species. Clearly, the predictions depend on whether genetic or demographic stochasticity is the more important factor in population decline (Dobson and Lyles, 1989). If genetic effects are more important, highly skewed reproduction associated with strong sexual selection will make populations vulnerable. On the other hand, if demographic stochasticity predominates, monogamous species may be worst off (Dobson and Lyles, 1989). More data on the mating system of *L. t. tardigradus*, obtained from both behavioural sampling and genetic analyses, and detailed demographic data, are needed in order to better evaluate the risk of extinction *L. t. tardigradus* populations face.

3. Improving forest patches: increasing area and creating corridors within a forest patch

The IUCN classed *Loris tardigradus tardigradus* as an Endangered (C2A(i)) subspecies based on the fact that there are less than 1500 animals across 3000 hectares of fragmented rainforest throughout the Wet Zone (IUCN, 2008). Much of the remaining forest patches in Sri Lanka are isolated from other patches, which presents an obvious problem to the viability of *L. t. tardigradus* populations inhabiting such forests. One solution would be to create corridors between patches. However, in most cases this may not be possible due to the distances that separate these patches and the presence of physical barriers such as roads and villages (see Figure 2.1). This is the case for MPFR. It is surrounded by four other forest patches of similar size, the closest being three kilometres away and the furthest one, four and a half kilometres away. It also is surrounded by major roads and village settlements. Connection to other forest patches would not be possible. Surveys conducted in 2002 and 2003 identified MPFR as having the highest density of lorises out of 19 other forest patches surveyed in the Wet Zone (Nekaris and Jayewardene, 2004). This may represent a stable situation as sufficient ecological resources may be available for now to sustain a relatively dense population. However, even if sufficient ecological resources are available, this small forest fragment of less than 300 hectares, would most probably not sustain a genetically viable population in the long term as the population contains only a small part of the original genetic variability (Cowlishaw and Dunbar, 2000). Inbreeding will affect reproductive success, sex ratio, mortality and susceptibility to diseases and environmental stress, making closed populations more likely to go extinct. A captive breeding program put in place in 1980 (Meier, 1989) with nine founding animals (five males and four females) from one natural breeding population

showed that although the colony successfully increased to a number of 36 individuals, animals were highly inbred. The outcome would be the same for a small, closed population in the wild, such as MPFR.

However, despite MPFR being a closed forest, the fragmentation within the forest, has resulted in the formation of smaller closed (to varying degrees) patches where loris sub-population occur (such as my study population). It thus seems that one conservation action that can be taken to ensure the long-term viability of the slender loris population in MPFR is to decrease fragmentation so as to increase movement within the forest and allow different individuals from semi-closed populations to disperse into new sub-populations (and thus increase genetic heterozygosity. As it is, the study site was practically (but not completely) isolated from other parts of the forest by a river, pine forest plantations and paddy fields. Paddy fields that were no longer actively managed were used in most cases as grazing fields. This prevented the regeneration of paddy fields into habitats that would become suitable for lorises. In abandoned paddy fields that were not used as grazing fields, grasses, shrubs and weeds were dense, particularly along the edges, as were seedlings and saplings. Such paddy fields were often used by lorises, for foraging and exploring activities. Restoration of abandoned paddy fields would not only serve the purpose of linking up forest patches within MPFR but also would expand the area within forest patches inhabited by lorises, thus decreasing competition for ecological resources. Introducing artificial perches and/or native fruiting trees, may facilitate succession in paddy fields by providing perches for birds (thus increasing seed dispersal), and buffering harsh microclimatic conditions, thus improving seedling survival (Zahawi and Augspurger, 1999).

During my time in MPFR, a programme by the European Commission (EC) and the United Nations Development Program (UNDP) (the Small Grants Program for Operations to Promote Tropical Forests) was set in place to promote sustainable forest management in direct partnership with local stakeholders. In 2005, five local NGOs were awarded micro capital grants to support community led initiatives, one of which is to convert pine forest plantations into natural forest by restoring the natural flora and fauna endemic to the area and conserving the forest with the involvement of the rural people. One of the targeted areas is MPFR, which will hopefully result in not only an increase in the total extent of natural forest, but also the conservation of its flora and fauna and a return to traditional forest management methods, such as the use of organic home gardens.

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sufficient ecological resources may be available for now to sustain a relatively dense population. However, even if sufficient ecological resources are available, this small forest fragment of less than 300 hectares, may not sustain a viable population in the long term (Cowlishaw and Dunbar, 2000). Forest patch size was reported as being strongly correlated with slender loris density (Nekaris, pers.comm.). It thus seems that one conservation action (and possibly the only action) that can be taken to ensure the long-term viability of the slender loris population in MPFR is to expand forest cover and decrease fragmentation so as to increase movement within the forest. As it is, the study site was practically isolated from other parts of the forest by a river, pine forest plantations and paddy fields. Paddy fields that were no longer actively managed were used in most cases as grazing fields. This prevented the regeneration of paddy fields into habitats that would become suitable for lorises. In abandoned paddy fields that were not used as grazing fields, grasses, shrubs and weeds were dense, particularly along the edges, as were seedlings and saplings. Such paddy fields were often used by lorises, for foraging and exploring activities. Restoration of abandoned paddy fields may thus be a way of expanding the area within forest patches inhabited by lorises and creating a habitat corridor within MPFR to allow slender lorises to move into other parts of the forest. Introducing artificial perches and/or native fruiting trees, may facilitate succession in paddy fields by providing perches for birds (thus increasing seed dispersal), and buffering harsh microclimatic conditions, thus improving seedling survival (Zahawi and Augspurger, 1999).

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4. Identifying habitat requirements of species of concern

In a complex dynamic environment where various factors, both behavioural and ecological, affect the decisions made by individuals, it may be difficult to evaluate preferred habitat. However, some choices are obvious without the need for complex analysis of multiple factors. In this study I have shown that lorises did not use home gardens, actively managed plantations or paddy fields. I have shown also that in the months when foliage is reduced, lorises decrease their activity, particularly when the moon is bright. These findings suggest that foliage cover may reduce the risk of predation, making this an important habitat requirement for *L. t. tardigradus*. This is supported by the fact that lorises regularly used abandoned pine forest plantations, which provide a safer habitat than actively managed plantations as a result of regenerating bushes and saplings providing cover and continuity for lorises (Kumara *et al.*, 2004). Similarly, as I mentioned in the previous section, abandoned paddy fields had regenerated to a point where lorises were able to move around and forage along the edges.

Due to their small size, lorises are restricted to having to use small substrates despite their ability to also use large substrates. The latter were not frequently used as it

clearly puts them at a disadvantage to predators. Thus, in terms of microhabitat structure, small substrates are essential to lorises. Connectivity between trees, in the form of lianas, also provides lorises with not only ways to travel between trees, but also, a way to escape predators. Lianas were frequently used also to travel vertically. Lorises at MPFR, despite preferring heights between three and five metres, often moved up to the top of the canopy (never more than 20 metres) and to the ground. Lianas provided lorises with a way to escape predators, as was observed once when one of the collared males was chased by a palm-civet. This may explain why lorises never used actively managed pine forests, where trees were not connected to each other and trunks would have been too large to allow rapid escape from a predatory attack. Pine trees on the edge of the forest were connected to other trees and thus were often used for foraging activities. Actively managed pine forests, home gardens and paddy fields all have one characteristic in common, open canopy with no understorey. This type of habitat would be dangerous for a loris to use not only because it results in a greater risk of being caught due to lack of connectivity, but simply because it increases the risk of being spotted by a predator. Boinski *et al.* (2003) found that despite equal amounts of predator abundance between habitats, the Bolivian squirrel monkey (*Saimiri boliviensis*) and the black crowned Central American squirrel monkey (*Saimiri oerstedii*) living in open habitats experienced a greater number of predator attacks per observed hour and showed a greater rate of preemptive predator vigilance than the common squirrel monkey (*Saimiri sciureus*) living in a closed canopy forest with a dense understory.

Despite making use of the most available microhabitat characteristics in MPFR, some intersexual differences on preferred plant species were found. This may have been a strategy to reduce competition between animals sharing a limited space, in this case,

adults of a spatial pair, and should be taken into account when choosing which plant species to use when restoring and regenerating forest patches.

5. Improving captive breeding, reintroduction, augmentation, and translocation programs.

Many reintroduction programs fail or have limited success because they neglect to account for the behavioural ecology of the species of concern. Some animals have an "innate" ability to recognize and avoid predators, while others must be taught predator avoidance (Caro, 1999), such as black-footed ferrets (*Mustela nigripes*). Understanding the behaviour of a species will help to ensure that proper training and conditioning is practiced before release. The first efforts to release golden lion tamarins (*Leontopithecus rosalia*) in the wild were largely unsuccessful because the animals lacked basic locomotory skills and the ability to recognize food or predators (Beck *et al.*, 1991). Captive breeding programmes can also be improved at the zoo facilities by recognising the importance of mate choice (Festa-Bianchet and Apollonio, 2003). In a study conducted on captive pygmy lorises (*Nycticebus pygmaeus*), the percentage of births was higher in pairs that had been kept together for more than 30 days before the female came into oestrous, than in pairs who were put together when females came into oestrous (Fitch-Snyder and Jurke, 2003), whilst a study on rates of pregnancies in captive grey mouse lemurs (*Microcebus murinus*) suggested that time for familiarisation, although not a general requirement, might be a factor influencing female reproduction (Radespiel and Zimmermann, 2003). In this study, males and females also formed pairs, both spatially and socially, and this may be a way for males to increase their chances of mating with the female. Breeding

slender lorises in captivity may thus require a male to be kept with a female for at least a month (as in the pygmy loris case) before the female reaches oestrous.

Breeding may also be affected by stress caused by visitors or other forms of disturbance within and around the exhibit. Studies in the wild provide a reference from which to monitor captive populations and evaluate their behaviour. For example, the vocal repertoire of *L. t. tardigradus* including contextual use of different call types could be used to evaluate the state of captive animals (Volodina, 2000). Acoustic studies conducted in the wild and in captivity to assess the degree of individual variation and better understand contextual use of different call types will contribute towards better captive management of species. For example, chitter calls were used by females rejecting advances by males and this information could be used as a way to assess compatibility between newly introduced pairs. In contrast, the use of low one tone calls, often used by females 'requesting' the attention of their male partner, would reflect formation of the pair-bond.

Translocation of slender lorises may become a necessary task in the future, either from captivity or from wild populations between forest patches. This can be a stressful experience for the animal and bad decisions could be fatal. Thus, detailed ecological data are required and ideally based on a sound knowledge of the species' biology, distribution and ecological requirements (Box, 1991; Kleiman, 1996; IUCN, 1998) and baseline data for reintroduction cannot be based on another species' ecological requirements, even if they are morphologically similar (e.g. *Loris lydekkerianus lydekkerianus*) (Streicher, 2004). Releasing a loris in broad daylight or even during a full moon in an area with little foliage cover (or at a time when foliage cover is low such as dry months), could put the animal at greater risk of predatory

attacks. Similarly, releasing the animal in an area with little substrate continuity prevents the animal from travelling easily and leaves little room for escape from predators. Releasing the animal during a month of little rain would put unnecessary pressure to find resources (Kleiman, 1996). Based on habitat and microhabitat characteristics used by lorises in this study, appropriate 'loris habitat' for release should consist of a combination of the following elements: thick foliage; high percentage connectivity between plants at all heights; frequency of at least two large trees per five metre radius, preferably fruiting trees such as *Artocarpus nobilis* to provide both shelter during rain, sleeping sites, and food (either the fruit or insects); presence of bushes and small trees, such as bamboo and *Humboldtia laurifolia*, to provide cover against predators, but also substrates of small sizes; evenly distributed food resources (either termite mounds, or plant species such as *H. laurifolia* and/or *Ochlandra stridula*); and in areas preferably away from human disturbance such as villages, village paths, monasteries, and actively managed plantations.

4.4.2. Conservation actions and proposals

1. Conduct a meta-analysis of past and current studies of *L. t. tardigradus*.
2. Model the distribution of *L. t. tardigradus* using ecological-niche modelling concepts and carry out a gap analysis to identify areas that should be given priority, for corridors and extension of protected areas.
3. Conduct process-based models such as PVAs (Population Viability Analysis) and metapopulation analysis to combine with habitat analysis.
4. Collect more data on social organisation, behavioural ecology and demography of different populations.

5. Conduct genetic analyses to determine mating system and genetic diversity of populations within small forest fragments.

6. Collect morphological and genetic data to confirm taxonomic status of *Loris lydekkerianus grandis*.

7. Improve small and isolated forest fragments, by increasing forest area and decreasing fragmentation: allow abandoned pine forest plantations and paddy fields to regenerate and actively plant native tree species to speed up the regeneration process and provide natural perches for birds (and thus increase seed dispersal). Create 'bridges' between trees along large village roads to prevent lorises from having to cross the road or travel a long way down to find connecting tree branches.

8. Increase protection of small forest fragments to create a large protected forest network and prevent further encroaching into existing forests.

CHAPTER 5 SUMMARY AND FUTURE RESEARCH

Several questions were raised in this study particularly in relation to the social organisation of *L. t. tardigradus*. It would be valuable to conduct genetic studies to assess relatedness within the MPFR population and work out whether EPCs are frequent or whether females only mate with the male of the social and spatial pair. The degree of sexual dimorphism and the relatively large testis size of loris males (and inter-male variation) suggest an element of polygyny with sperm competition, as proposed for *L. l. malabaricus* (Kar-Gupta, 2007), but testis size variation may also be related to breeding seasonality. Several questions were raised in this study on the presence of breeding seasonality as evidence points to two potential mating seasons. This thesis provided some indication of potential home range enlargement during times of oestrous but whether they constitute strong enough pressures for the observed social and spatial patterns remains to be tested. Future studies looking specifically at shifts of core areas (for both males and females), changes in home range size, movement (path length walked) along the home range boundary, frequency of encounters with neighbouring animals, and vocalisations, during times of oestrous would help understand the reproductive strategies employed by male and female lorises. The mating system of *L. t. tardigradus* is unlikely to be truly monogamous but more evidence is needed to firmly refute this argument. What is certain is that the social organisation exhibited by *L. t. tardigradus* is more flexible and complex than had previously been suggested for the slender loris, as elements of both a unimale-unifemale system and a multimale-multifemale system are shown. The way pairs form currently remains a mystery. Do females move into the home range of a lone male? Or do females settle into an unused area and advertise their sexual status to attract

males into their home range? How much choice do females have in the partner with whom they share a home range and what constitutes the basis for such choices? Radio-tracking for periods of more than one year would reveal the strength of the pair bond as well as the dispersal patterns of both males and females. Females may disperse when they are nulliparous, as was the case with one of the subadult females FG, but the event of female FB dispersing with a newborn raises the question about age at dispersal and reasons for dispersal. Do males disperse at a younger age than female and how does this affect the operational sex ratio and subsequent male-male competition? Unlike the study by Kar Gupta (2007) where some males roamed significantly larger areas than settled males, in this study no males showed such ranging patterns and little difference in home range size was found between males, whether they were settled and paired, or unpaired.

Kar Gupta (2007) reported condition-dependent tactics by males to attract females with paired males being in better condition and able to monopolise good habitat, thus appearing more attractive to females. Could this be an effective reproductive strategy employed by males to monopolise females and sire most offspring at MPFR? In future studies the collection of data on body condition based on Kar Gupta's (2007) index of male condition would be necessary to investigate such intra-sexual differences in relation to whether the male is paired or unpaired and combine such data with paternity analyses and observational data on mating. In MPFR, the habitat was heterogeneous, but differences in food availability between areas of different floristic composition and structure were not investigated. Whether the habitats within home ranges of pairs provide better food availability and quality than habitats of unpaired males and females would need to be investigated by conducting systematic and

intensive insect surveys using a combination of trapping methods within the home ranges of paired and unpaired animals.

Slender lorises have shown some degree of ecological plasticity in the fact that they made use of most frequent microhabitat features within forested areas. However, they showed little plasticity in habitat use by the fact that they did not make use of the extra space provided by plantations, agricultural fields and home gardens, as reported for *L. lydekkerianus* despite little forested space available. Such habitat preference limits the extent of space available to slender lorises and increases the effect of fragmentation, resulting in lorises not being able to disperse within a forest patch fragmented by agricultural fields and plantations, as was the case in MPFR. The lack of dispersal of animals belonging to such a small population could result in the population becoming unviable. It is vital that steps are taken to first and foremost decrease fragmentation within forest patches such as MPFR, before focussing on creating large-scale wildlife corridors across Sri Lanka's Wet Zone. Some patches, such as MPFR, would not even meet the criteria as it is isolated from other forest patches by main roads and villages. The only hope left for such forest patches within Sri Lanka's Wet Zone, is to increase the quality of that forest to allow increased dispersal routes for lorises and increased forested space.

I propose that Masmullah Proposed Forest Reserve serve as a site of future study to investigate: 1) slender loris density estimates; 2) the social organisation of the slender loris, building on the existing database from this study; 2) habitat quality within and outside slender loris home ranges; 3) forest dynamics and correlate changes to forest structure and floristic composition to slender loris population densities and movements; 4) predator densities and dynamics to better understand the effect of predation on loris behaviour and population dynamics and 5) I also propose that

conservation efforts take place in MPFR by: 1) regenerating abandoned pine forest plantations and agricultural plantations; 2) creating small corridors to allow slender lorises to reach different parts of the forest if separated by actively managed plantations; agricultural fields or roads and 3) conducting thorough and systematic biodiversity surveys to investigate changes over time and 4) to bring MPFR and surrounding small forest patches under the protected area network of Sri Lanka.

Designating MPFR as a forest reserve and an official study site by the Departments of Wildlife, the Forest Department and the Ministry for the Environment, would be a major step in the conservation of *L. t. tardigradus*, its habitat and other species inhabiting it. In the longer term, future studies such as this one should be conducted in areas with different ecological characteristics (forest patch size, degree of fragmentation, degradation and human disturbance, predation levels, resource abundance and distribution) to determine how each of these factors may influence the dynamics of *L. t. tardigradus* behaviour and density so that appropriate conservation strategies may be proposed.

APPENDIX 1

VEGETATION SAMPLING FORMULAS

Shannon-Weiner's Index of Diversity:

$$'H' = -\sum_{i=1}^{S} (P_i)(\ln P_i)$$

H = the symbol for the diversity in a sample of S species

S = the number of species in the sample

P_i = relative abundance of ith species and is equal to n_i/N, where

N = the total number of individuals of all species

n_i = the number of individuals of ith species

ln = the natural log

Simpson's Concentration of Dominance:

$$'D' = -\sum_{i=1}^{S} (P_i)^2$$

D = the symbol for the concentration of dominance in a sample of S species

S = the number of species in the sample

P_i = relative abundance of ith species and is equal to n_i/N, where

N = the total number of individuals of all species

n_i = the number of individuals of ith species

Sorensen's Index of Similarity:

$Q/S = [2j / (a+b)] \times 100$

Q/S = the symbol for the quotient of similarity between two samples

a = the total number of species in sample 1

b = the total number of species in sample 2

j = the number of species common to both samples

Tree Basal Area:

Basal Area of a tree (m^2) = (DBH/200)2 x 3.142

DBH is the diameter of the tree at breast height

APPENDIX 2

MORPHOLOGICAL MEASUREMENT DATA SHEET

FOR SLENDER LORISES CAUGHT IN THE WILD

Examination by: _____

Date of examination: _____

Time at start of examination: _____

Time at end of examination: _____

Examined animal

Radio-collar frequency: _____

Name of animal: _____

Sex: _____

Weight: _____

Estimated age: _____

Estimated age based on: _____

Condition of animal: _____

Reproductive status: _____

Site where animal caught: _____

Habitat where animal caught: _____

Body measurements (mm)

	Left	Right
Upper arm (humerus)		
Forearm (radius)		
Upper leg (femur)		
Lower leg (tibia)		
Hand length		
Hand span		
Foot length		
Foot span		
Ear width		
Ear length		

Other measurements:

Neck circumference: _____

Body length: _____

Muzzle length: _____

Face width (maximum breadth over postorbital bars): _____

Head breadth: _____

Description of animal

Marking and pigmentation

Colour of circumocular patches: _____

Presence of rim around eyes: _____

Colour of median facial stripe: _____

Shape and size of median facial stripe: _____

Colour of dorsal stripe: _____

Shape and size of dorsal stripe: _____

Part of body where most prominent: _____

Pigmentation of ears: _____ muzzle: _____

Hands and feet: _____

Fur colour and quality

General colour: _____

Dorsal hairs

Colour: _____

Colour of base: _____

Frosting: _____

Quality: (woolly?stiff?wavy?curly?dense?)_____

Length: _____

Ventral hairs

Colour: _____

Colour of base: _____

Frosting: _____

Quality: _____

Length: _____

Limbs, hands and feet hairs

Colour: _____

Frosting: _____

Quality: _____

Length: _____

Genitalia

Female

Vaginal cleft opening and colour: _____

Description of nipples: _____

Male

Penis length: _____

Testicle width (right and left): _____

Testicle length (right and left): _____

Scrotal pigmentation: _____

Behaviour

Behaviour during examination: _____

_____

Breaths per minute before examination and after examination:

_____

Other

Data sheet designed by Lilia Bernede on 10.03.2006.

APPENDIX 3

MORPHOLOGICAL MEASUREMENTS

ID	Sex	Examina-tion time (mins)	Travel time (mins)	Weight (gr)	Body length (mm)	Forearm	Upper arm	Hand span	Hand length	Lower leg	Upper leg	Foot span	Foot length
FJ	female	28	14	111	179	59.4	39.3	33.2	/	74.2	62.8	28.9	/
FF	female	35	6	133	153	47.3	28.9	20.1	24.2	73.0	72.0	31.6	32.3
FE	female	40	6	153	235	65.0	53.9	34.4	48.9	68.8	64.3	41.0	30.9
FB	female	45	12	117	193	68.0	52.3	/	/	65.4	65.0	46.4	32.2
FI	Female	30	10	114	233	66.0	54.3	33.1	23.4	68.1	70.5	/	/
FG	female	45	42	114	230	67.0	55.0	34.0	25.0	71.5	72.0	37.0	35.8
FK	female	38	14	149	191	67.3	55.8	28.5	25.3	71.0	70.0	40.0	36.8
FM	female	35	44	129	203	69.6	50.0	34.2	24.4	70.5	68.0	45.5	38.5
FR	female	43	0	110	189	61.5	48.5	25.0	25.0	64.0	66.0	41.5	35.0
MJ	male	42	24	160	157	68.9	47.3	/	/	71.7	55.1	34.9	/
MA	male	30	24	150	188	63.4	/	23.6	24.6	64.0	50.9	31.9	29.6
MD	male	47	6	171	183	62.8	43.5	/	21.8	68.2	65.6	38.3	27.2
Ma	male	45	30	150	221	64.7	56.0	/	28.8	64.7	73.0	28.3	31.2
MT	male	45	14	144	202	67.0	42.1	34.1	26.6	63.5	64.0	/	/
MC	male	35	10	138	205	64.0	53.5	/	/	71.9	67.3	46.7	40.8
MH	male	40	6	124	185	66..5	55.8	31.3	25.5	69.3	71.3	36.5	35.5
MO	male	60	6	139	203	67.0	59.5	30.5	27.0	72.5	76.0	43.0	40.0
ML	male	63	44	142	189	65.5	62.5	34.5	26.5	71.5	71.0	43.0	36.5
MJ1	male	17	0	30	130	/	/	/	/	/	/	/	/
MJ2	male	15	16	75	171	/	/	/	/	/	/	/	/
MJ3	male	15	14	71	.169	/	/	/	/	/	/	/	/

APPENDIX 3 continued

MORPHOLOGICAL MEASUREMENTS continued

D	Sex	Face width	Head breadth	Muzzle length	Ear length	Ear width
FJ	female	/	/	/	/	/
FF	female	/	13.6	11.1	12.2	12.0
FE	female	39.8	26.4	9.1	8.9	11.2
FB	female	37.5	23.8	14.0	9.1	13.1
FG	female	36.0	28.0	14.1	8.0	12.5
FK	female	35.5	23.0	10.3	11.8	15.0
FM	female	36.0	20.0	12.0	12.5	12.5
FR	female	33.0	26.0	11.5	13.0	9.3
MJ	male	38.3	33.0	/	/	/
MA	male	/	/	/	/	/
MD	male	/	26.5	12.7	/	10.4
Ma	male	40.4	30.0	10.4	/	12.2
MT	male	41.7	27.3	12.8	/	17.0
MC	male	36.0	24.9	12.7	13.1	12.8
MH	male	33.0	20.5	6.5	10.0	8.8
MO	male	37.0	21.0	12.0	11.5	13.5
ML	male	39.0	25.	13.0	19.5	15.5

APPENDIX 3 continued

AGE DEFINING CHARACTERISTICS

	FEMALES					
ID - age	**Weight (g)**	**Coat condition and colour**	**Pigmentation of ears**	**Teeth quality**	**Facial markings**	**Reproductive characteristics**
FR – subadult	110	Good - pale coat colour	Bright yellow.	Sharp and white	No rim around circumocular patches	Anoestrous, nulliparous
FJ – subadult	111	Good - pale coat colour	Bright yellow.	Sharp and white	No rim around circumocular patches	Anoestrous, nulliparous
FG – subadult	114	Pale yellow-reddish coat	Bright yellow.	Sharp and white	Light rim around circumocular patches	Anoestrous, nulliparous
FI – adult	116	Pale reddish coat – grey hairs on face	Pale yellow/ pink.	Sharp and white	Dark rim around circumocular patches	Anoestrous, nulliparous
FB – adult	117	Pale reddish coat	Pale yellow/ pink.	Sharp and white	Dark rim around circumocular patches	Anoestrous, primiparous
FM – adult	129	Dark reddish coat – some grey hairs	Pale yellow/ Pink.	Sharp and dark	Dark rim around circumocular patches	Oestrous, nulliparous
FF – adult	133	Dark grey-reddish coat – grey hairs on face	Greyish yellow	Worn and dark	Dark rim around circumocular patches	Anoestrous, multiparous
FK – adult	149	Pale reddish coat	Greyish yellow	Worn and dark	Dark rim around circumocular patches	Oestrous, multiparous
FE – adult	153	Dark grey-reddish coat – grey hairs on face	Greyish yellow	Worn and dark	Dark rim around circumocular patches	Anoestrous, multiparous

	MALES					
ID - age	**Weight (g)**	**Coat condition and colour**	**Pigmentation of ears**	**Teeth quality**	**Facial markings**	**Reproductive characteristics**
MH – adult	124	Pale reddish coat	Pale yellow/ pink.	Sharp and dark	Dark rim around circumocular patches	Visible scrotal pigmentation
MC - adult	138	Dark grey-reddish coat	Pale yellow.	Sharp and dark	Dark rim around circumocular patches	Visible scrotal pigmentation
MO – adult	139	Dark grey-reddish coat	Pale yellow/ pink.	Sharp and dark	Dark rim around circumocular patches	Visible scrotal pigmentation
ML – adult	139	Dark grey-reddish coat	Pale yellow/ pink.	Sharp and dark	Dark rim around circumocular patches	Visible scrotal pigmentation
MT – adult	144	Dark grey-reddish coat – grey hairs on face	Greyish yellow	Sharp and dark	Dark rim around circumocular patches	Visible scrotal pigmentation
MA – adult	150	Dark reddish coat	Pale yellow/ pink	Sharp and dark	Dark rim around circumocular patches	Visible scrotal pigmentation
Ma – adult	150	Dark grey-reddish coat	Greyish yellow	Sharp and dark	Dark rim around circumocular patches	Visible scrotal pigmentation
MJ – adult	160	Dark grey-reddish coat – grey hairs on face	Greyish yellow – lots of black spots	Worn and dark	Dark rim around circumocular patches	Visible scrotal pigmentation
MD – adult	171	Dark grey-reddish coat – grey hairs on face	Greyish yellow	Worn and dark	Dark rim around circumocular patches	Visible scrotal pigmentation

APPENDIX 3 Continued

BIRD BANDS USED TO MARK JUVENILES

APPENDIX 4

A Comparison of Home Range Estimators using Telemetric Data on the Red Slender Loris (*Loris tardigradus tardigradus*) in Masmullah Proposed Forest Reserve, Sri Lanka.

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KEY WORDS: *Loris tardigradus*, Lorisidae, home range, MCP, KDE, core area

Introduction

Radio-tracking, or wildlife telemetry, is a technique that has revolutionised wildlife research and increased our knowledge of animal behaviour and ecology. There is no other wildlife research technique that comes close to approximating its many benefits (Mech, 1983). Since the beginnings of radio-tracking, the development of radio telemetry techniques has enormously influenced the direction of wildlife research and at least one hundred papers are now published each year on radio-tagged wildlife (Kenward, 2001). Because of the diversity of applications that it offers, it presents an almost unlimited potential for learning new information and is a method that is now ubiquitous in studies of wild animals (Samuel and Fuller, 1994)

This increase in analytical techniques used to estimate ranging patterns (see Harris *et al.*, 1990; White and Garrot, 1990 for reviews), has resulted in researchers not always being able to compare their findings due to the lack of consensus regarding techniques for measuring spatial characteristics (home range size, core area size, home range overlap) (Sterling, *et al.*, 2000; Bearder, 1987). The method used to estimate home range size, shape and internal structure, have a significant effect on results obtained (Harris *et al.*, 1990). Currently, a wide choice of methods exist for estimating home

range boundaries and internal cores (e.g. Dixon and Chapman, 1980; Anderson, 1982; Geissler and Fuller, 1985; Samuel and Garton, 1985; Kenward, 1987; Worton, 1989, 1995a; Loehle, 1990). The methods differ in ability to distinguish core areas as well as outer boundaries, estimate shapes that conform to the observed pattern, or in the number of locations per range needed to achieve reliable estimates (Kenward, 1992). The earliest, most intuitive and still most commonly used method of estimating home range size is the minimum convex polygon (MCP; Mohr, 1947; Seaman *et al.*, 1999) which provides estimates by connecting the outermost location points, thus forming a convex polygon representing the animal's home range (Harris *et al.*, 1990). This method thus fails to distinguish internal structure and may overestimate home range size (Kenward *et al.*, 2001). Nevertheless, if animals do not have multiple core areas, consistently sleep along range boundary and make regular and predictable movements, then this method may be suitable (Pimley, 2002). Another type of link distance method, known as between nearest neighbour locations, can be used in cluster analysis to estimate size, shape and structure of home ranges (Kenward, 2001).

Another 'family' of methods used to estimate home range is based on densities of locations. One example is the kernel method which assesses an animal's probability of occurrence at each point in space. Kernel estimators are one of the many nonparametric methods of estimating densities, and have been available for several decades (Millspaugh and Marzluff, 2001). It is only relatively recently though that this method has been evaluated (Worton, 1987, 1989; Powell *et al.*, 1997; Seaman and Powell, 1996; Swihart and Slade, 1997; De Solla *et al.*, 1999; Seaman *et al.*, 1999) and used as a method for estimating animal home ranges (e.g. Pimley, 2002; Newton-Fisher, 2003; Wong, *et al.*, 2004). The kernel method's popularity appears largely due to its proven ability to outperform its precursors in Monte Carlo simulations (Worton,

1995; Seaman and Powell, 1996) and provision of greater internal range resolution through an integrated utilization distribution (UD) function (Worton, 1987, 1989, Silverman, 1986). It is typically reported as the minimum area that includes a fixed percentage of the estimated utility distribution volume (Millspaugh and Marzluff, 2001). However, despite gaining in popularity for estimating home range characteristics, this method has been criticized with regards to the smoothing factor used to calculate contours, in some cases resulting in overestimation of home range size as with the MCP method (Wauters *et al.*, 2007). The literature is contradictory on this subject with some authors suggesting the use of LSCV to calculate the smoothing factor and others recommending the use of a reference smoothing factor.

With such a variety of methods to choose from it is no surprise that no consensus has been reached as to which method to use. Kenward (2001) recommend the use of both density and linkage estimators of home range until a basis for a priori choices has been made for the particular study and animal being studied, whilst Wauters *et al.* (2007) recommend the use of both MCP and KDE for home range size and KDE for core area size. They also recommend using the clusters analysis (85%) method for estimating core areas when animals have multinuclear ranges and MCP (85%) when the range is mononuclear.

Thus, in this study I compared four methods of analysis in an attempt to identify which ones best estimate and describe ranging patterns in the red slender loris at MPFR and also to allow future studies on this species to follow similar methodology, and for comparisons to be made. I use two analytical methods based on link distances between locations (MCP and cluster analysis) and two based on densities of locations (Kernel with LSCV and Kernel with a ref smoothing factor multiplied by 0.75). The

aim of this is to identify which method of home range analysis is best suited to the ranging patterns exhibited by the red slender loris in MCP.

Methods

Data collection and analysis

We radio-tracked seventeen adult slender lorises between August 2005 and August 2006, with an average of 20.7 ± 13.6 track nights and 603.1 ± 506 fixes per animal (Table 1). We allocated equal efforts to increasing the number of animals radio-collared and the number of fixes collected for each animal in order to obtain a representative sample of the existing population and provide a reliable estimate of home range size for each individual, respectively (Millspaugh and Marzluff, 2001).

Home range areas were estimated using Ranges 7 home range analysis package (Kenward, 1990). I used four methods of home range analysis: the Minimum Convex Polygon (MCP) and cluster analysis (Mohr, 1947; Kenward, 1987) and the Kernel Density Estimators (KDE) with the more widely used LSCV calculated h value (h_{lscv}) and with h_{ref} multiplied by 0.75 to achieve a realistic estimate comparable across individuals. The multiplier 0.75 was chosen by visually comparing home range contours obtained with different h_{ref} values (Worton, 1987, 1989; Powell *et al.*, 1997, Wauters *et al.*, 2007). I estimated the number of fixes needed to obtain a reliable estimate by plotting fixes against home range size until they reached an asymptote on the area-observation curve (e.g. Gese *et al.*, 1990). Four of the radio-collared animals were not tracked long enough to allow an asymptote to be reached. Those were excluded from analysis.

TABLE 1. Number of individuals radio-tracked, their sex and age (AF = subadult female, AF = adult female, AM = adult male), the number of hours tracked, location points and months followed.

ID	Age-Sex	Tracking days	Fixes	Sleeping sites	Months	Circumstances
FE	AF	35	1168	50	Dec 05 – Jun 06	
FF	AF	15	327	10	Sep 05 - Nov 05	Signal stopped after 3 months. Disappeared.
FB	AF	38	1639	47	Dec 05 - May 06	Dispersed in April with infant
FI	AF	26	1057	29	Jan 06 - May 06	
FG	SAF	22	1059	19	Feb 06 - Jun 06	
FK	AF	25	691	15	Mar 06 - Jun 06	
FM	AF	15	346	7	Apr 06 - Jun 06	
FR	SAF	3	37	2	Jul 06 - Aug 06	Lost radio-collar
FJ*	SAF	NA	72		Nov 05 - Dec 05	Not radio-collared
MJ	AM	19	486	19	Aug 05 - Dec 05	
MA	AM	11	303	9	Aug 05 - Sep 05	
Ma	AM	4	89	3	Oct 05	Signal interference
MD	AM	33	625	46	Aug 05 – Feb 06	
MT	AM	48	1525	48	Nov 05 - May 06	
MC	AM	3	55	3	Nov 05	Disappeared
MH	AM	19	681	20	Mar 06 - Jun 06	
MO	AM	18	611	10	Apr 06 - Aug 06	
ML	AM	5	85	6	Apr 06 - May 06	Lost radio-collar
J1	JM	NA	NA		May 06 - Jun 06	Not radio-collared
J2	JM	NA	NA		Jan 06	Not radio-collared
J3	JM	NA	NA	3	Jun 06	Not radio-collared
21	9♀ 9♂	339	10767	346	Aug 05 – Aug 06	

Home range analyses

Autocorrelation

The MCP and KDE methods of estimating home range size are robust to some autocorrelation, with the latter not requiring serial independence of locations (Millspaugh and Marzluff, 2001; De Solla *et al.*, 1999). Numerous studies report that sub-sampling does not reduce autocorrelation of location points and that home range size, partitioning and total distance traveled, are better represented by auto-correlated observations (Reynolds and Laundre, 1990; Swihart and Slade, 1997; De Solla *et al.*, 1999; Otis and White, 1999). Animal movement patterns are not random or temporally independent by nature, so analysing a statistically independent dataset may not provide a realistic description of what is essentially a non-independent phenomenon (Lair, 1987). For the purpose of this study I chose to include all location points, which were taken at constant time intervals for each individual, in order to increase accuracy and precision.

Home range size

I defined an animal's total home range area and identified home range overlap based on estimates obtained using the KDE method with a probability of use of 0.95, thus excluding occasional excursions. Contours were fitted to locations using a smoothing factor h of 0.75. The number of fixes used to identify core area was identified using a utilisation distribution curve of home range sizes calculated using the KDE method. I assessed (by eye) the point at which the curve's steepness sharply decreases (Figure 2.8).

Based on the curve shown in figure 2.8, it seems that the core area for lorises should consist of 85% of fixes as percentage increase of home range size relative to total home range size, sharply increases after that point.

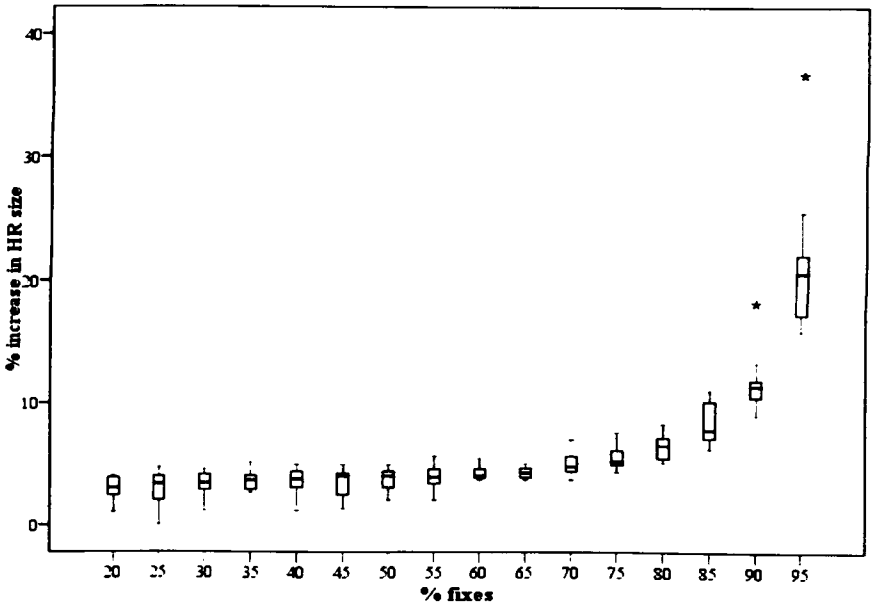


Figure 2.9. Utilisation distribution curve of median percentage increase in home range size as the number of fixes used to calculate home range (using KDE) increases, for 13 radio-collared individuals.

Autocorrelation: The belief that radio-tracking location points must not be autocorrelated, but instead should be statistically independent from each other, has been the topic of debate for at least two decades (Swihart and Slade, 1985a, b; Thomas and Taylor, 1990). Some believe that autocorrelation of locations causes negatively biased estimates of home range size (Swihart and Slade, 1985a) and thus, location fixes should be independent of each other. This is achieved by using location points separated by a certain time interval (Time To Independence, TTI), so that successive locations cease to be significantly correlated (Swihart and Slade, 1985a). However, it has been counter-argued that by definition, the concept of a home range (as defined by Burt, 1943) involves autocorrelated movements (Otis and White, 1999)

as animal movement patterns are not random or temporally independent by nature, and therefore, analysing a statistically independent dataset may not provide a realistic description of what is essentially a non-independent phenomenon (Lair, 1987). Many thus argue that subsampling of data to achieve a TTI between points, may not only fail to reduce autocorrelation of location points, but causes redundancy in the data and significant underestimation of home range size and rates of movements (Rooney *et al.* 1998; De Solla *et al.*, 1999; Otis and White, 1999; Swihart and Slade, 1997; Reynolds and Laundre, 1990). Thus, I chose to include all location points available in my analyses, which were all taken at the shortest time interval possible (five minutes), so that the best possible estimation of home range size and use could be obtained and comparability between individuals made possible (Rooney *et al.* 1998; Otis and White, 1999).

Results

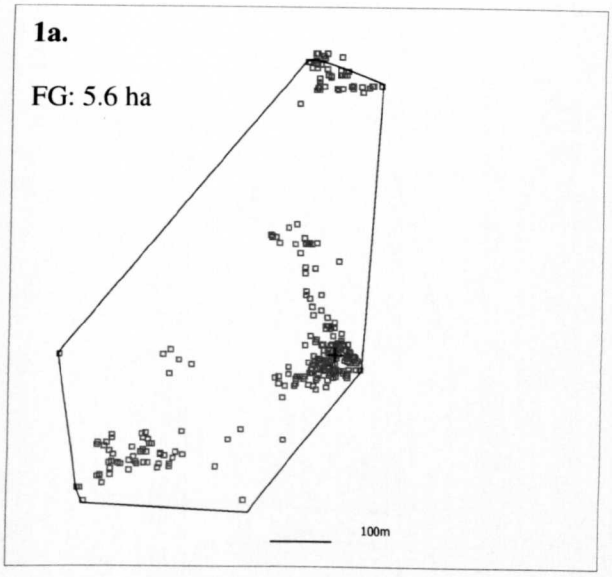
Total home range size

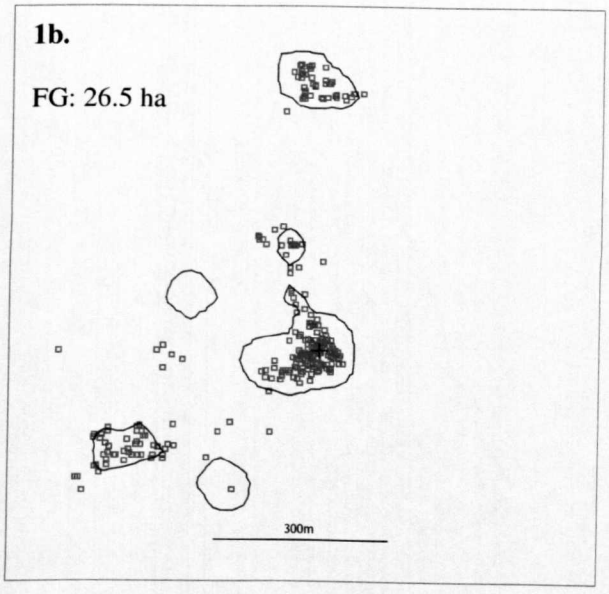
Table 2 presents total home range sizes obtained for each individual (n = 13) using four different methods. Home ranges estimates were the largest for most individuals (n = 10) with the MCP method, followed by estimates obtained using KDE with LSCV calculated smoothing factor, followed by estimates obtained using KDE with reference smoothing factor multiplied by 0.5. The smallest estimates were obtained with the nearest-neighbour linkage method.

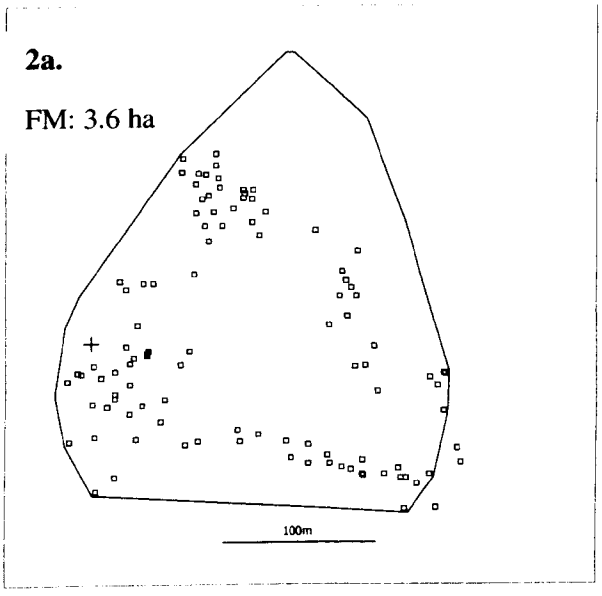
TABLE 2. Home range estimates (ha) for 12 adults and 1 subadult (FG) measured using MCP (95%), nearest-neighbour cluster analysis (95%) and KDE (95%) with two different smoothing factors. The mean and standard deviation are given for all animals and for the 12 adults only (excluding sub adult female).

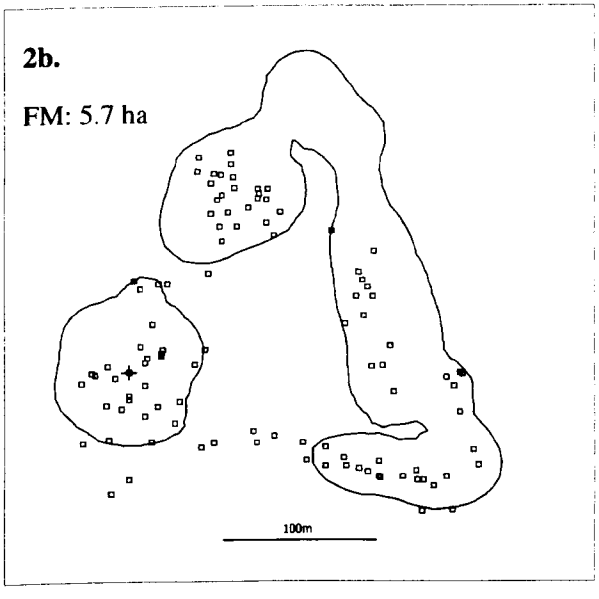
ID	Fixes	MCP	Nearest-neighbour clusters	KDE with h_{lscv}	KDE with $h_{refx0.75}$
FB	1639	7.61	1.03	4.61	2.78
FG	1059	26.49	2.12	12.47	6.92
FF	327	3.58	1.62	3.07	2.45
FI	1057	7.44	1.28	5.78	5.36
FK	691	3.27	0.88	2.79	2.43
FM	346	5.69	2.61	5.33	4.51
FE	1168	1.70	0.77	1.23	1.22
MJ	486	1.98	1.14	1.30	1.39
MH	681	1.97	1.22	2.06	1.91
MA	303	1.84	1.12	1.33	1.40
MD	625	3.47	2.72	3.83	3.37
MO	611	5.25	1.93	5.38	4.12
MT	1525	3.50	2.42	3.33	3.11
Mean ± SD	809 ± 443	5.7 ± 6.6	1.6 ± 0.7	4.0 ± 3.0	3.2 ± 1.7
Mean ± SD *without FG*		3.9 ± 2.1	1.6 ± 0.7	3.3 ± 1.7	2.9 ± 1.3

In some cases home range size was greatly over-estimated by the MCP method (figures 1a, 1b and figures 2a, 2b). Similarly, the KDE with LSCV created 'over-smoothed' contours, thus increasing the area beyond a realistic estimate. The nearest-neighbour linkage method resulted in the smallest home range estimates. A good compromise between the above three methods is the KDE with a smoothing factor multiplied by 0.75, which gave the most realistic estimates.


1a.
FG: 5.6 ha
100m


1b.
FG: 26.5 ha
300m





Figures 1a. and 2a show sub-adult FG's and adult FM's home ranges (respectively) estimated with MCP, and figures 1b and 2b, show home ranges estimated with KDE.

The extreme home range value for the subadult FG was removed from analysis to avoid undue leverage of statistical values. Home range sizes estimated by MCP (Mean = 3.6 ha $\pm$ 2.1) were significantly larger than home range sizes estimated by KDE $h_{ref \times 0.75}$ (Mean = 2.3 ha $\pm$ 1.2) (paired t-test: t 2.940, d.f. = 11, p = 0.013).

Core area size

Table 3 shows the core area estimates using MCP and KDE with $h_{ref \times 0.75}$ both based on 85% of fixes, and core area estimated from sleeping site locations only using MCP (100%). The 85% MCP method overestimated core areas by including areas never used by the animal. Core areas based on sleeping sites only were on average close to core area estimates obtained with the KDE (85%) method (paired t-test: 0.027, d.f. = 12, p = 0.979). However, for nine of the individuals, core area including sleeping sites alone was smaller than core area based on an 85% utilization probability. For three of the females with multiple cores, the estimates based on sleeping sites alone were larger than those obtained from 85% KDE.

TABLE 3. Individual core area sizes for 12 adults and 1 sub-adult (FG). Core areas were estimated using: all location fixes (with 85% MCP and 85% KDE) and using sleeping site locations (with MCP). The mean and standard deviation are given for all animals and for the 12 adults only (excluding sub adult female).

ID	Age and sex	Core areas	MCP (85%)	Sleep sites (MCP 95%)	KDE $_{hrefx0.75}$ (85%)
FB	AF	1	2.33	1.33	2.2
FG	SAF	5	23.2	13.16	3.95
FF	AF	2	2.92	0.12	1.67
FI	AF	2	5.95	4.99	3.76
FK	AF	2	2.85	1.84	1.67
FM	AF	3	5.09	0.58	3.15
FE	AF	1	1.15	0.34	0.86
MJ	AM	1	1.48	0.88	0.87
MH	AM	1	1.54	0.97	1.23
MA	AM	1	2.85	0.34	0.93
MD	AM	1	4.60	1.14	2.71
MO	AM	1	3.90	0.70	3.03
MT	AM	1	2.83	1.85	2.50
	Mean $\pm$ SD		4.7 $\pm$ 5.8	2.2 $\pm$ 3.5	2.2 $\pm$ 1.1
	Mean $\pm$ SD *without FG*		3.1 $\pm$ 1.5	1.3 $\pm$ 1.3	2.0 $\pm$ 1.0

Discussion

In this study I tested different methods of estimating home range size and core area size for *Loris tardigradus tardigradus* in MPFR. In this case, the MCP and the KDE with LSCV calculated smoothing factor, resulted in overestimates of home range size. As shown by the examples of the dispersing female FB and the female FM whose home range surrounded a paddy field, MCP includes areas rarely used by the animal and in doing so increase home range size. The KDE method solves this problem by measuring the home range based on density of locations. Thus, it will less likely include areas not used by the animal. This study also shows that the value of h has a considerable influence on the home range estimate and varies according to the number of fixes. When using KDE, LSCV has been widely recommended to calculate bandwidth (e.g. Kenward, 2001; Gitzen and Millspaugh 2003). Visual inspection of home range contours revealed that the smoothing factor calculated with LSCV resulted in most cases in an overestimate of home ranges. Home ranges reached an accurate estimate (again based on visual inspection of contours) when I multiplied the reference smoothing factor by 0.75. This value was a good compromise for all home ranges. A similar method was used by Pimley (2002) to choose the appropriate smoothing factor for fixed-kernel calculations. Cluster analysis greatly underestimated home range size. Whereas KDE will calculate the entire area within one large contour enclosing areas with a certain probability of use (in this case 95%), clusters are treated separately and areas in between ignored. Even if an animal uses these areas between clusters of high location density, it should nevertheless be considered as part of the animal's home range. For this reason, cluster analysis may only be useful to investigate pattern of range use (Kenward, 1987), rather than obtain estimates of total home range size.

When measuring core area size, the distinction between mono- and multinuclear home ranges is fundamental in choosing which method of home range analysis should be used. For animals with one core area, the MCP method may be the best option, but for animals with more than one core area, the MCP will overestimate this core area, as was the case for females in this study who had multiple core areas. The MCP may also be suitable where animals consistently sleep and forage along their range boundary and where they make regular and predictable movements. One way to potentially avoid these pitfalls is to only include sleeping site fixes. Researchers often gather data on home range patterns using sleeping site locations (Bearder and Martin, 1980, Harcourt and Nash, 1986, Schwab, 2000). In this study, the average core area estimated using this method did not differ from the average core area estimate obtained using the more reliable KDE and thus may prove to be a reliable and quick method of estimating average core area size (provided that enough individuals are sampled so as to dilute any effects of unusual individual circumstances, such as FG's movement patterns). However, for the purpose of estimating areas most intensively used by animals, and not only relating to sleeping sites but also preferred foraging areas, and for the additional purpose of being able to compare those across the population, the KDE method proved to be the better of the three methods for estimating core area size and use.

In summary, I found that to estimate total home range size, core area size, and home range use, by lorises at MPFR, the KDE method, with a chosen reference bandwidth based on visual inspection of home range shape and knowledge of areas known to be used or never frequented by the animals, provided the most accurate estimate.The MCP overestimated home range size, particularly for dispersing animals, animals with several core areas, and animals whose home ranges surrounded an unused area. The

same was true for KDE with LSCV which resulted in 'over-smoothing' the contour surrounding areas of high location density. Cluster analysis also did not provide realistic estimates and largely underestimated home range size. However, like the KDE, it was useful for describing home range patterns of use. The disadvantage with the density-based methods is the difficulty in comparing home range sizes between studies as each program uses different set of algorithms and a different grid-cell size (Harris *et al.*, 1990).

It is inevitable that with an increase in radio-tracking studies, variability with regards to radio-tracking methodology, spatial analysis and computer program used also will increase and result in comparability between studies to become more and more difficult. The only way to avoid this problem is for researchers to describe in detail the methodology, and parameters of analysis (Sterling, 2000; Pimley 2002, Bearder, 1987). Harris *et al.* (1990) revealed that out of 92 radio-tracking studies on mammals, 72 did not justify the methods used, out of 94 studies, 69 only used one analytical method (the majority, MCP), that the number of fixes for an asymptote to be reached was not given 62 out of 82 studies and finally, that autocorrelation was not considered or justified in 79 out of 81 cases. What this highlights is the lack of discipline and scientific rigor when it comes to detailing the methodology used in radio-tracking studies. Thus, I propose that the following details be given so as to permit different studies to be compared:

- Number of fixes collected for each animal;
- Time spent radio-tracking;
- Whether fixes were taken at regular intervals or not (continuous vs. discontinuous tracking); How fixes were taken and whether all fixes were used

in analysis and if not, justify; the number of fixes needed to reach asymptote for each individual;

- Method of analysis used;
- Number of analytical methods used (ideally more than one);
- How core areas were estimated and why; and for each analytical method, to detail the parameters of analysis (e.g. smoothing factor, how it was calculated, grid cell size, programme used, etc)

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APPENDIX 5

PHOTOGRAPHS OF SLENDER LORIS FACES

FEMALES

FB

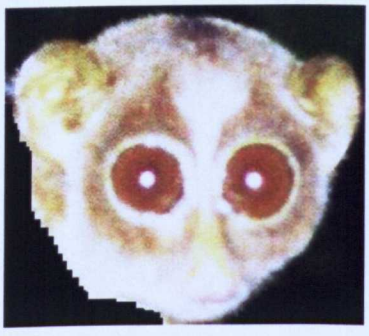
FE

FF

FK

FG

FM



FI

MALES

MA

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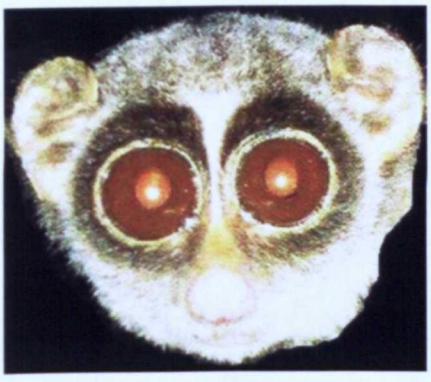

MD

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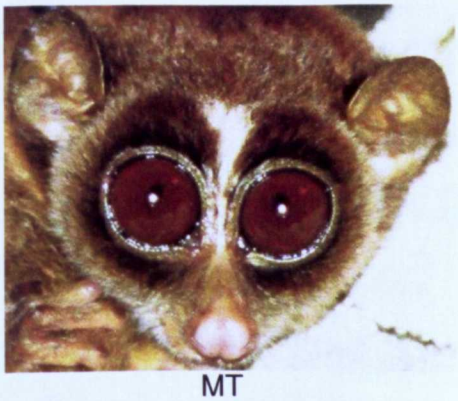

MT

APPENDIX 6

LIST OF PLANT SPECIES RECORDED AT MPFR

E = endemic, N = native, I = introduced. The sites/habitats where the tree species are typically found are as follows: RF = rainforest; MF = monsoonal forest; IF = intermediate forest; SF = secondary forest; FE = forest edge; HG = home gardens; Coast = coastal areas. The forest level in which species are typically found is given when known: c = canopy; sc = subcanopy; us = understorey. Information on origin of species and site is based on Ashton *et al.* 1997 and Peradeniya Botanical Gardens

Species – Latin name	**Sinhalese name**	**Origin**	**Tree type**	**Family**
Actephila excelsa	Otha	E	RF us.	Euphorbiaceae
Alstonia scholaris	Ruk athena	N	MF/RF	Apocynaceae
Alstonia macrophylla	Hawary nuga	I	SF	Apocynaceae
Anisophyllea cinnamomoides	Welipiyanna	E	RF c.	Rhizophoraceae
Aporusa lindleyana	Kebella	N	RF us.	Euphorbiaceae
Ardisia willisii	Baludang	E	Coast	Myrcinaceae
Artocarpus heterophyllus	Kos	E	HG	Moraceae
Artocarpus nobilis	Badidel	E	IF/RF c. sc. HG	Moraceae
Barringtonia aisatica	Duna mudilla	N	HG	Lecythidaceae
Berrya cordifolia	Halmilla	N	MF c.	Tiliaceae
Bhesa ceylanica	Pelen	E	RF c.	Celastraceae
Borassus flabellifer	Panai	E	Coast	Palmae
Bombax ceiba	Katu embula	N	MF/IF/RF c.	Bombaceae
Bridelia retusa	Ketakale	N	MF/IF sc	Euphorbiaceae
Bridelia moonii	Pathkala	E	RF us.	Euphorbiaceae
Canarium zeylanicum	Kekuna	E	RF c.	Burseraceae
Canthium dicoccum	Poromale	E	MF/IF sc. RFus.	Rubiaceae
Carallia brachiata	Dawate	N	RF sc.	Rhizophoraceae
Chaetocarpus castanocarpus	Hedawake	N	RF sc. us.	Euphorbiaceae
Chrysophyllum roxburghii	Kohola lavulu	I	MF/IF sc. RFus.	Sapotaceae
Dillenia retusa	Godapara	E	SF scrub	Dilleniaceae
Dillenia triquetra	Diyapara	E	SF scrub	Dilleniaceae

Dimocarpus longan	Mora	N	MF/IF sc. RFus.	Sapindaceae
Diospiros racemosa	Kaluwella	N	RF sc. us.	Ebenaceae
Dipterocarpus zeylanicus	Hora	E	RF c.	Dipterocarpaceae
Eugenia bracteata	Tambale	N	SF/IF	Myrtaceae
Erythroxyum zeylanicum	Hanun kirilla	E	MF/IF us.	Erythroxylaceae
Fahrenheitia zeylanica	Otha	N	RF us.	Euphorbiaceae
Ficus fergusonii	Kos Gonna	E	RF sc. us.	Moraceae
Garcinia quaesita	Goraka	E	IF/RF us. HG	Clusiaceae
Gyrinops walla	Walla pateka	N	RF us.	Thymelaeceae
Gyrinops walla?	Walle	N		Thymelaeceae
Horsfieldia iriyaghedhi	Ruk	E	RF sc.	Myristicaceae
Horsfieldia irya	Iriya ruk	N	RF sc.	Myristicaceae
Humboldtia laurifolia	Gal karanda	N	RF us.	Leguminosae
Lagerstroemia speciosa	Mavrutha	N	FE, HG	Lythraceae
Lijndenia capitellata	Piniboru	E	RF us.	Melastomataceae
Litsea iteodaphne	Bomiya	E	RF sc. us.	Lauraceae
Macaranga peltata	Kenda	N	SF	Euphorbiaceae
Mangifera zeylanica	Etamba	E	IF/RF c.	Anacardiaceae
Mastixia tetrandra	Diyaheliya	E	RF sc.	Cornaceae
Memecylon capitellatum	Welikaha	E	MF/RF us.	Melastomataceae
Mesua nagassarium	Natau	N	IF/RF c. HG.	Clusiaceae
Ochlandra stridula	Bamboo/Bata	E	RF/SF/FE	Gramineae
Ochna lanceolata	Bokeralle	N	MF/IF/RF us.	Ochnaceae
Operculina turpethum	Tholol	I	SF	Convolvulaceae
Palaquium thwaitesii	Kirihambiliya	E	RF us.	Sapotaceae
Palaquium petiolare	Kirihambiliya	E	RF c.	Sapotaceae
Polyalthia korinti	Ul kenda	N	SF	Annonaceae
Prunus walkeri	Gulumora	N	RF sc. SF.	Rosaceae
Schumacheria	Kekiriwara	E	RF/FE	Dilleniaceae

castaneifolia				
Semecarpus walkeri	Badulla	E	RF sc.	Anacardiaceae
Semecarpus subpetata	Kabara badulla	E	RF sc.	Anacardiaceae
Semecarpus sp.	Maha badulla	E	RF sc.	Anacardiaceae
Semecarpus sp.	Heen badulla	E	RF sc.	Anacardiaceae
Semecarpus sp.	Badulla wage	E	RF sc.	Anacardiaceae
Sterculia balanghas	Nawapatte	N	IF c.	Sterculiaceae
Swietenia macrophylla	Mahogany	I	IF, FP, HG	Melliaceae
Vitex altissima	Milla	N	MF/IF c/sc	Verbenaceae
Rukgaha; Mugunawak; Molambe; Adenate; Borca; Kahapenda; Kirinda; Eepetha; Walkebella				

APPENDIX 7

LIST OF TREE SPECIES SURVEYED AND THEIR IMPORTANCE VALUE INDICES

Species	Relative density	Relative frequency	Relative basal area	Importance Value Index (IVI)
Humboldtia laurifolia	0.133	0.869	0.198	**1.200**
Swietenia macrophylla	0.039	0.616	0.078	**0.733**
Dipterocarpus zeylanicus	0.057	0.539	0.136	**0.732**
Artocarpus nobilis	0.036	0.496	0.062	**0.594**
Semecarpus walkeri	0.022	0.523	0.018	**0.563**
Mangifera zeylanica	0.026	0.489	0.011	**0.525**
Dillenia retusa	0.029	0.379	0.117	**0.525**
Actephila excelsa	0.008	0.364	0.011	**0.383**
Horsfieldia iriyaghedhi	0.022	0.302	0.024	**0.348**
Bhesa ceylanica	0.005	0.315	0.028	**0.348**
Canarium zeylanicum	0.017	0.224	0.044	**0.285**
Gyrinops walle	0.011	0.188	0.005	**0.203**
Prunus walkeri	0.014	0.187	0.002	**0.202**
Chaetocarpus castanocarpus	0.009	0.188	0.001	**0.198**
Bridelia retusa	0.008	0.133	0.005	**0.146**
Mesua nagassarium	0.007	0.109	0.027	**0.143**
Alestonia scholaris	0.013	0.103	0.019	**0.133**
Garcinia quaesita	0.007	0.125	0.000	**0.132**
Canthium diccocum	0.014	0.112	0.001	**0.126**
Dimocarpus longan	0.005	0.106	0.011	**0.122**
Horsfieldia iriya	0.005	0.100	0.005	**0.110**
Artocarpus heterophyllus	0.004	0.063	0.032	**0.099**
Lijndenia capitellata	0.004	0.088	0.002	**0.093**
Memecylon capitellatum	0.009	0.081	0.001	**0.091**
Gyrinops sp.	0.005	0.075	0.008	**0.088**
Lagerstroemia speciosa	0.006	0.075	0.007	**0.088**
Anisophyllea cinnamomoides	0.005	0.078	0.001	**0.083**
Carallia brachiata	0.009	0.053	0.010	**0.072**
Dillenia triquetra	0.014	0.056	0.001	**0.070**
Vitex altissima	0.012	0.053	0.002	**0.067**
Sterculia balanghas	0.002	0.056	0.004	**0.063**
Ardisia willisii	0.003	0.056	0.001	**0.061**
Ficus fergusonii	0.004	0.053	0.000	**0.057**
Polyalthia korinti	0.004	0.050	0.001	**0.055**
Mastixia tetrandra	0.003	0.050	0.001	**0.054**
Diospiros racemosa	0.013	0.028	0.000	**0.040**
Bridelia moonii	0.003	0.025	0.010	**0.038**
Bombax ceiba	0.001	0.031	0.003	**0.035**
Semecarpus sp.	0.010	0.025	0.001	**0.035**
Palaquim twaitesii	0.003	0.031	0.001	**0.035**

Semecarpus sp.	0.003	0.028	0.000	**0.031**
Palaquim petiolare	0.002	0.028	0.001	**0.030**
Litsea iteodaphne	0.003	0.025	0.001	**0.029**
Berrya cordifolia	0.002	0.025	0.001	**0.028**
Semecarpus sp.	0.003	0.025	0.000	**0.028**
Erythroxyum zeylanicum	0.001	0.025	0.000	**0.026**
Schumacheria castaneifolia	0.001	0.025	0.000	**0.026**
Chrysophyllum roxburghii	0.001	0.025	0.000	**0.026**

APPENDIX 8

LIST OF MAMMAL SPECIES RECORDED AT MPFR AND

THEIR IUCN CONSERVATION STATUS

Species name	Family	Common name	IUCN conservation status
Felis viverrina	Felidae	Fishing cat	Vulnerable C2a(i)
Felis rubiginosa	Felidae	Rusty-spotted cat	Vulnerable C2a(i)
Paradoxurus zeylonensis	Viverridae	Golden palm-civet	Vulnerable B1ab(i,iii,v)
Paradoxurus hermaphroditus	Viverridae	Common palm-civet	Least Concern
Viverricula indica	Viverridae	Small Indian civet	Least Concern
Herpestes focus	Herpestidae	Indian brown mongoose	Vulnerable A2c
Lutra lutra	Mustelidae	Eurasian otter	Near Threatened
Hystrix indica	Hystricidae	Indian crested porcupine	Least Concern
Moschiola meminna	Tragulidae	White-spotted chevrotain	Least Concern
Sus scrofa	Suidae	Eurasian wild boar	Least Concern
Trachypithecus vetulus	Cercopithecidae	Purple-faced langur	Endangered A2cd+3cd+4cd
Macaca sinica	Cercopithecidae	Toque macaque	Endangered A2cd
Loris tardigradus	Lorisidae	Red slender loris	Endangered C2a(i)
Ratoufa macroura	Sciuridae	Giant squirrel	Near Threatened
Funambulus palmarum	Sciuridae	Common squirrel	Least Concern
Funambulus pennantii	Sciuridae	Five-striped squirrel	Least Concern
Bandicoot indica	Muridae	Greater bandicoot rat	Least Concern
Mus cervicolor	Muridae	Ceylon field mouse	Least Concern

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